Eesti Maaülikool
Estonian University of Life Sciences

UNDERSTOREY VEGETATION AND FACTORS AFFECTING IT IN YOUNG DECIDUOUS FOREST PLANTATIONS ON FORMER AGRICULTURAL LAND

ALUSTAIMESTIK JA SEDA MÕJUTAVAD TEGURID ENDISTEL PÕLLUMAJANDUSMAADEL KASVAVATES NOORTES LEHTPUUISTANDIKES

TEA TULLUS

A Thesis
for applying for the degree of Doctor of Philosophy in Forestry

Väitekiri
filosoofiadoktori kraadi taotlemiseks metsanduse erialal

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which are referred to by the Roman numerals in the text. The papers are reproduced by the kind permission of the publishers.

I **Soo, T**., Tullus, A., Tullus, H., Roosaluste, E. 2009. Floristic diversity responses in young hybrid aspen plantations to land-use history and site preparation treatments. Forest Ecology and Management, 257, 858–867.

II **Soo, T**., Tullus, A., Tullus, H., Roosaluste, E., Vares, A. 2009. Change from agriculture to forestry: floristic diversity in young fast-growing deciduous plantations on former agricultural land in Estonia. Annales Botanici Fennici, 46 (4), 353–364.

III **Tullus, T**., Tullus, A., Roosaluste, E., Tullus, H. 2012. Bryophyte vegetation in young deciduous forest plantations. Baltic Forestry, 18(2), 205–213.

IV **Tullus, T**., Tullus, A., Roosaluste, E., Kaasik, A., Lutter, R., Tullus, H. 2013. Understorey vegetation in young naturally regenerated and planted birch (*Betula* spp.) stands on abandoned agricultural land. New Forests, doi.: 10.1007/s11056-013-9365-9.

The contributions from the authors to the papers were as follows:

	I	**II**	**III**	**IV**
Original idea	HT, ER, TT	TT, AT	TT	TT
Study design	TT, ER, HT	TT, ER, HT, AV	TT	TT
Data collection	TT, ER	TT, ER	TT	TT, ER, RL
Data analysis	TT, AT	TT, AT	TT, AT	TT, AK, AT
Preparation of the manuscript	All	All	All	TT, AT, HT, ER

AK – Ants Kaasik, AT – Arvo Tullus, AV – Aivo Vares, ER – Elle Roosaluste, HT – Hardi Tullus, RL – Reimo Lutter, TT – Tea Tullus (prev. Soo), All – all authors of the paper

ABBREVIATIONS

BA	Stand basal area
D'	Simpson's diversity index
DBH	Diameter at breast height
DCA	Detrended Correspondence Analysis
MRPP	Multiresponse Permutation Procedures
NMDS	Non-metric Multidimensional Scaling
S	Species richness
SRF	Short-rotation forestry

1. INTRODUCTION

During the past decades a considerable area of agricultural land has been abandoned in Northern and Eastern Europe (Peterson and Aunap, 1998; Kuemmerle *et al.*, 2011; Alcantara *et al.*, 2012). Historically, agricultural lands have mainly been established on previous forest lands in the region. For example, in Estonia forests covered ca 85% of the land 2500–3000 years ago, when human impact on forests was insignificant (Laasimer, 1965). Thus the afforestation of currently existing abandoned agricultural land is in accordance with natural vegetation succession. At the same time there exist two alternative strategies for afforestation, depending on whether the final goal is to create a natural forest with minor human impact or to initiate intensive production of woody biomass (or a certain wood assortment) – i.e. to establish a productive forest plantation. The establishment of forest plantations on former agricultural land can satisfy the demand for industrial timber and woody biomass as a renewable energy resource, at the same time reducing the timber harvest from natural forests (Tullus *et al.*, 2012b). Therefore, a growth in the area of forest plantations has occurred in Europe since 1990 (FAO, 2006b). In plantations with fast growing deciduous trees the concept of short-rotation forestry (SRF) with rotation periods less than 30 years can be applied (Tullus *et al.*, 2013).

Although the main goal of commercial forest plantations is the production of timber and bioenergy, the implications for biodiversity (including floristic diversity) can not be neglected (Carnus *et al.*, 2006; Stephens and Wagner, 2007; Brockerhoff *et al.*, 2008; Baum *et al.*, 2009; Bremer and Farley, 2010). The studies concerning the impact of forest plantations on biodiversity that have been carried out in different regions of the world have often arrived at contradictory conclusions. Even-aged monocultural forest plantations are sometimes seen as ecological deserts, offering habitat only for a small number of ecologically less valuable species. Therefore it is important to monitor the biodiversity of Estonian forest plantations. It is a subject that has not been thoroughly studied in Estonia before.

The history of afforestation of former agricultural lands in Estonia dates back to the beginning of the 19^{th} century (Laas, 2004). Considering that the forest cover has increased from its lowest documented value of

20% (Etverk and Sein, 1995) at the beginning of the 20th century to the currently estimated 50.6% (Aastaraamat Mets, 2012), this means that more than half of the forests in Estonia today are growing on former agricultural lands and can be regarded as semi-natural, meaning that their creation has comprised of both natural and assisted regeneration. The main planted species have been conifers, while deciduous forests have, as a rule, evolved through natural forestation. However, the history of intensively managed forest plantations and SRF is much shorter. Since the 1990s the following tree species have been planted on former agricultural lands: hybrid aspen (more than 700 ha) (Tullus, 2010), curly birch (ca 500 ha) (Sibul *et al.*, 2011), spruce as Christmas trees (ca 400 ha) (Sirgmets and Vahter, 2009), willow for bioenergy (ca 40 ha) (Heinsoo and Holm, 2008). More seldom other tree species such as silver birch, alders, ash and oak have been planted. Conifers are generally less favoured for SRF due to slower initial growth, more acid litter, higher fire hazard, larger risk of spreading root rot and less vegetative regeneration possibilities. Hybrid aspen (*Populus* × *wettsteinii* Hämet-Ahti = *P. tremula* L. × *P. tremuloides* Michx.) is a new deciduous tree species for Estonian forestry, as its large-scale cultivation started in 1999. Besides a study conducted in an exhausted oil shale quarry in Estonia (Tullus *et al.*, 2008), the impact of hybrid aspen on understorey vegetation has not previously been studied in Estonia and has only briefly been analysed together with other fast-growing poplar plantations on former arable land in Germany (Heilmann *et al.*, 1995) and Sweden (Weih *et al.*, 2003). Hybrid aspen is a semi-exotic species for Estonia, as *P. tremula* is indigenous and *P. tremuloides* originates from North America. Although *P. tremula* and *P. tremuloides* are genetically close species (Cervera *et al.*, 2005), some ecological differences have been observed between European aspen and hybrid aspen in Scandinavia and the Nordic countries, including differences in the phenology and growth speed during the first 15–20 years (Yu *et al.*, 2001; Heräjärvi and Junkkonen, 2006) and different susceptibility to some pests and diseases (Kasanen *et al.*, 2002). The understorey vegetation of hybrid aspen plantations is the main topic of paper **I** in the current thesis and a subtopic of papers **II** and **III**, where vascular plant and bryophyte understorey characteristics are comparatively studied between hybrid aspen and silver birch (*Betula pendula* Roth) plantations.

Birches (*Betula pendula* and *B. pubescens*) are the most wide-spread and economically significant deciduous trees in our region (Hynynen *et al.*, 2010). Birches can be grown in forest plantations on former agircultural land (Johansson, 1999; Liepins, 2007), where a shorter rotation period can be recommended than in traditional forestry (Tullus *et al.*, 2012a). In addition to forest plantations established through planting, abandoned agricultural areas are reforested through the process of secondary succession, with pioneer species (e.g *Betula* spp) among the first arrivers. The comparison of understorey vegetation characteristics between naturally regenerated and planted deciduous stands in abandoned agricultural sites (the topic of paper **IV**) has not been previously studied in Estonia.

The current thesis concentrates on the understorey vegetation (vascular plants and bryophytes) of forest plantations on abandoned agricultural lands. The following aspects are analysed: main site and stand factors affecting understorey vegetation characteristics in young plantations (**I–IV**); the impact of hybrid aspen, as a semi-exotic tree species, on the understorey in comparison with native tree species silver birch (**II**, **III**); the formation of the forest understorey in stands and plantations of birch and in SRF plantations with hybrid aspen growing on former agricultural land (**I**–**IV**); the formation of the bryophyte layer in hybrid aspen and silver birch plantations (**III**); the comparison of understorey vegetation characteristics between silver birch plantations and naturally regenerated birch stands (**IV**).

2. REVIEW OF THE LITERATURE

2.1. Plantation forestry

According to the Global Forest Resources Assessment report 2005 (FAO, 2006a) plantations are forests of introduced species and in some cases native species, established through planting or seeding, with few species, even spacing and/or even-aged stands. The area of plantations was estimated as 3.8 percent (140 million hectares) of the world's total forest area in 2005. Productive forest plantations, primarily established for wood and fibre production, accounted for 78 percent of forest plantations, and protective forest plantations, primarily established for conservation of soil and water, for 22 percent (FAO, 2006a).

In 2010, in the same report, the new concept of planted forests was introduced, uniting plantation forests and planted semi-natural forests that were formerly considered separately (FAO, 2006b; FAO, 2010). Planted forests are defined as forests established through planting and/or through seeding of native or introduced species in the process of afforestation or reforestation. In 2010 the area covered by planted forests accounted for 7 percent of total forest area and was increasing steadily.

Resulting from the expansion of plantation forestry, more attention has been paid to the environmental impacts of this kind of land use. Over the last decade a series of review articles and reports have been published addressing the biodiversity issues of forest plantations (Hartley, 2002; Carnus *et al.*, 2006; Stephens and Wagner, 2007; Brockerhoff *et al.*, 2008; Baum *et al.*, 2009; Bremer and Farley, 2010; Felton *et al.*, 2010; Hartmann *et al.*, 2010) and trying to answer the question whether plantations have a positive or negative impact on biodiversity. The results are nevertheless controversial and differ between different taxonomic groups. Additionally, the impact of the establishment of forest plantations on biodiversity is influenced by the type of land-use that the plantation replaces (Christian *et al.*, 1994; Bremer and Farley, 2010) or is compared with. The landscape context (forest or agricultural) is important as well (Weih *et al.*, 2003; Weih, 2008).

Biodiversity in forest plantations is also influenced by the choices made in the establishment phase and management (site preparation methods, use of herbicides and fertilizers, monocultures *versus* polycultures, native species *versus* exotics, short rotations *versus* longer rotations and harvesting regimes) (Hartley, 2002). Generally, the use of native species is recommended, as the risks of spreading new plant diseases and genetic contamination of the local species pool are excluded. Additionally, a number of species (especially invertebrates and microorganisms) may be adapted only to native trees (Hartley, 2002) and the use of exotic tree species would exclude them. According to the review compiled by Bremer and Farley (2010) native species plantations were more species rich than the paired secondary forests, while exotic species plantations were less species rich than the paired secondary forests. But once again, the results may be different for different taxonomic groups such as lichens, bryophytes, fungi, vascular plants, invertebrates and songbirds (Quine and Humphrey, 2010). Although vascular plants colonize plantations regardless of the identity of canopy species (Carnus *et al.*, 2006), some studies have indicated a higher share of exotic plant species in the undestorey of plantations with exotic tree species (Brockerhoff *et al.*, 2003., Chytrý *et al.*, 2005; Mascaro *et al.*, 2008; Paritsis and Aizen, 2008).

2.2. Understorey vegetation in forest plantations on former agricultural land

In Estonia the establishment of forest plantations is seen as one way to reemploy abandoned agricultural sites (Jõgiste *et al.*, 2003; Vares, 2005; Tullus *et al.*, 2007; Tullus, 2010). Studies concerning the understorey vegetation of plantations on former agricultural land (former fields, improved grasslands and unimproved grasslands, pastures) have targeted SRF plantations as well as plantations that are managed in longer rotations. The majority of the studies have concentrated on vascular plants; bryophytes have received less attention. Given the fact that a continuous understorey of bryophytes and lichens is characteristic of boreal forests (Longton, 1992), the formation of the bryophyte layer should also be studied in boreal plantations. Moreover, earlier studies (e.g Herben, 1987; Ingerpuu *et al.*, 1998, 2001, 2003; Hokkanen, 2006) have indicated that bryophytes and vascular plants may respond differently to environmental factors, which can be related to the significant differences in the morphology and physiology of these plant groups.

The understorey of SRF plantations is characterised by Heilmann *et al.* (1995) for Germany and Gustafsson (1987, 1988) and Weih *et al.* (2003)

for Sweden. Characterization of phytodiversity in German and Swedish short-rotation coppice plantations and a review article concerning the understorey of SRF plantations is provided by Baum *et al.* (2009, 2012a, 2012b). Floristic diversity is also included in the studies addressing the ecology of SRF plantations (e.g. DTI 2004, 2006; Fry and Slater, 2009, for the UK, NABU, 2008 for Germany and Weih, 2008 for Nordic and Baltic countries.) In general, changes in the understorey vegetation are governed by the changes in the canopy cover. The older the trees and the closer they are planted, the more shaded is the understorey, leading to the replacement of light-demanding and short-lived species by shade tolerant perennials. In addition, root competition with trees impacts understorey development. When compared to arable fields the species richness in SRF plantations has been found to be higher (Heilmann *et al.*, 1995; Baum *et al.*, 2009; Baum et al., 2012a) or on the same level but with a different species composition (Weih *et al.*, 2003). In comparison with old-growth mixed deciduous forests the species richness has been found to be similar or lower (Weih *et al.*, 2003). In the long run, repeated short-rotational harvests may reduce the populations of many forest species that are not adapted to frequent disturbances (Halpern and Spiess, 1995; Weih *et al.*, 2003).

Understorey vegetation is also analysed in the studies that address the influence of afforestation on grasslands: Buscardo *et al.*, 2008 for Ireland; Alrababah *et al.*, 2007 for Jordan; Maccherini and De Dominicis, 2003 for Italy; O'Connor, 2005 for South Africa. The studies in afforested Irish grasslands and the semi-arid Mediterranean grasslands of Jordan show that afforestation represents a threat to semi-natural habitats where distinctive plant communities may occur (Buscardo *et al.*, 2008; Alrababah *et al.*, 2007).

On the other hand, there are several studies concerning the effect of plantations on the restoration of floristic diversity and flora typical to native forests (Geldenhuys, 1997; Lemenih and Teketay, 2005; Newmaster *et al.*, 2006; Brunet, 2007; Aubin *et al.*, 2008; French *et al.*, 2008; Calviño-Cancela *et al.*, 2012; Boothroyd-Roberts *et al.*, 2013) or characterizing understorey development towards a forest (Bråkenhielm, 1977; Hill and Jones, 1978; Rūsiņa *et al.*, 2011). In general, the restoration of flora typical to native forest may be a long process in the areas once cleared for agricultural purposes; the reasons for this are discussed in the next section.

2.3. Agricultural legacy

Understorey vegetation of forests that have developed on former agricultural land differs from the vegetation of ancient forests (Hermy, 1994; Petersen, 1994; Graae and Sunde, 2000; Singleton *et al.*, 2001; Bellemare *et al.*, 2002; Flinn and Vellend, 2005; Flinn and Marks, 2007; Hermy and Verheyen, 2007). Agricultural land use impacts soil chemical and physical properties: higher pH as a result of liming, higher nutrient concentrations (especially of phosphorus) (Koerner *et al.*, 1997; Honnay *et al.*, 1999; De Keersmaeker *et al.*, 2004; Falkengren-Grerup *et al.*, 2006) and lower organic matter content compared to the soils under continuous forest cover (Flinn and Vellend, 2005; Valtinat *et al.*, 2008). These differences become less apparent over time (Flinn and Marks, 2007), but in some cases they have been evident even centuries later (Dupouey *et al.*, 2002).

Forest species generally have low seed persistence (Thompson *et al.*, 1998; Bossuyt and Hermy, 2001) and, since agricultural land use depletes the seed bank of forest plants, the recovery of forest understorey vegetation requires recolonization by forest species. Migration rates of forest species are usually quite low (Dzwonko and Loster, 1992; Brunet and Oheimb, 1998; Bossuyt *et al.*, 1999; Bossuyt and Hermy, 2000; Dzwonko, 2001; Graae *et al.*, 2003), causing differences in the species composition of understorey vegetation of recent forests bordering on ancient forest and isolated recent forests (Dzwonko, 1993). The ability of understorey species to colonize recent forests displays interregional variation (De Frenne *et al.,* 2011). In addition to the dispersal limitations (Brunet and Oheimb, 1998; Brunet *et al.*, 2000; Jaquemyn *et al.*, 2001; Graae *et al.*, 2003), some authors have pointed to the recruitment problems of forest species caused by site quality variables (e.g soil properties) or exclusion by competitive species (Honnay *et al.*, 1999; Verheyen *et al.*, 2003; De Keersmaeker *et al.*, 2004). Post-dispersal seed predation of woody forest species has also been cited as a possible factor explaining limited restoration (Bruun *et al.,* 2010).

Secondary succession on afforested land is also influenced by the type of former agricultural use (Koerner *et al.*, 1997; Ito *et al.*, 2004; Wulf, 2004; Brunet, 2007; Kopecký and Vojta 2009). Several studies have demonstrated the differences in the species composition of forests with different agricultural land use histories. In the study from northeastern Germany more woodland species and more endangered or relatively rare species occurred in the afforestations on former grasslands than in woodlands created on arable fields (Wulf, 2004), suggesting that afforestations should preferably be established on former grasslands. Brunet (2007) observed that southern Swedish broadleaved forests established on former fields more frequently included acid-sensitive species than forests on former pastures, indicating the long-term effect of liming in the fields. In the study compiled in French spruce plantations Koerner (1997) found that former pastures as well as old forests were characterized by a higher frequency of acidophilic or low-nitrogen-demanding species; forests in previous croplands and gardens were characterized by a high frequency of nitrophilic species.

2.4. Forest plantations *versus* naturally regenerated stands

Agricultural sites that are left unused become afforested in the process of secondary succession. Although economically significant stand growth and yield characteristics may be better in plantations established with previously selected planting material than in naturally regenerated stands, studies conducted in former mining areas have highlighted the advantages of natural succession, such as more diverse vegetation (Pensa *et al.*, 2004), higher understorey species richness and diversity (Hodačova and Prach, 2003) and a higher proportion of rare and endangered species (Tropek *et al.*, 2010; Prach *et al.*, 2011). On abandoned agricultural lands, understorey vegetation characteristics in plantations and in naturally regenerated stands have rarely been comparatively studied (Aubin *et al.*, 2008; Zhang *et al.*, 2010; Boothroyd-Roberts *et al.*, 2013). As abandoned agricultural sites cover a considerable area in Northern and Eastern Europe (Peterson and Aunap 1998; Kuemmerle *et al.*, 2011; Alcantara *et al.*, 2012), such comparisons are necessary.

3. AIMS AND HYPOTHESES OF THE STUDY

Main aims:

1. To determine which site- and stand-related factors have affected understorey vegetation characteristics (species composition, species richness) in young commercial forest plantations on abandoned agricultural land (**I–IV**);
2. To study if plantations of semi-exotic hybrid aspen offer similar habitat for the understorey as plantations of native tree species silver birch (**II, III**);
3. To characterize the formation of the bryophyte layer and provide ecological characterization of bryophyte species common to young deciduous plantations (**III**);
4. To characterize the formation of forest understorey in young first-generation forests growing on former agricultural land (**I–IV**);
5. To compare understorey vegetation characteristics between naturally regenerated birch stands and silver birch plantations (**IV**).

Hypotheses:

1. Understorey vegetation reflects the influence of former disturbances (previous agricultural land use, site preparation method) (**I, III**);
2. Understorey vegetation characteristics are similar in native silver birch and semi-exotic hybrid aspen plantations (**II, III**);
3. The share of forest species (vascular plants and bryophytes) is low in the understorey vegetation of plantations on former agricultural land (**I–IV**);
4. Naturally regenerated stands support higher understorey species richness than plantations (**IV**).

4. MATERIALS AND METHODS

4.1. Study area

The study comprises 24 commercial hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) plantations, 11 silver birch (*Betula pendula* Roth) plantations and 11 naturally regenerated birch (*B. pendula* Roth and *B. pubescens* Ehrh.) stands all situated on former agricultural land in Estonia. The majority of the stands are situated in the continental part of Estonia, with an exception of one silver birch plantation and two naturally regenerated birch stands on the islands of Hiiumaa and Saaremaa (Figure 1).

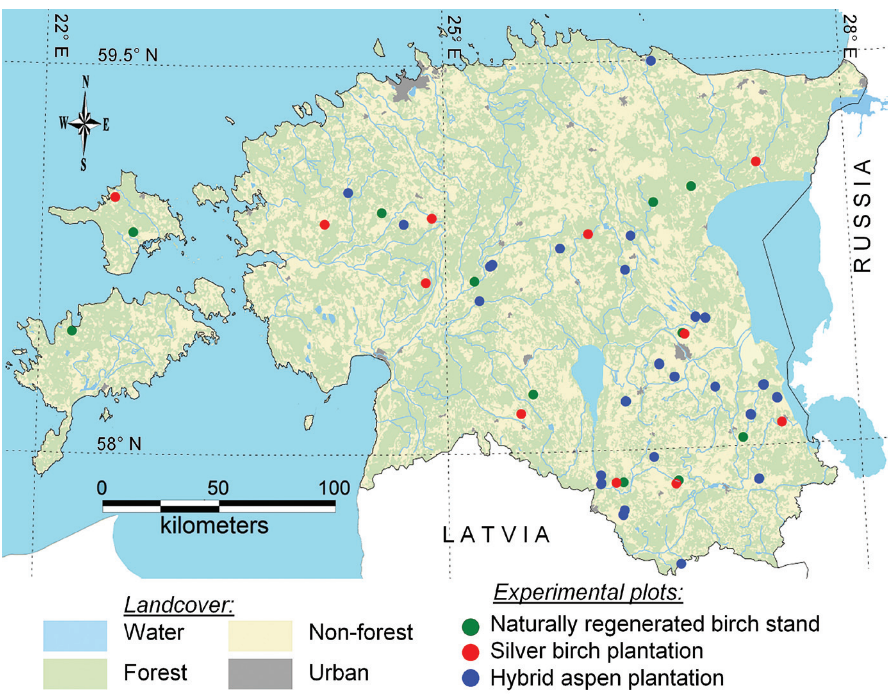

Figure 1. Locations of the studied hybrid aspen and silver birch plantations and naturally regenerated birch stands in Estonia.

The purpose of the hybrid aspen and silver birch plantations is the production of pulp- and energywood. The predicted rotation period is 20–30 years for hybrid aspen (Tullus *et al.*, 2012b). The legitimate felling age of silver birch in Estonian forests is 60–70 years (Metsa majandamise eeskiri, 2010), but in plantations on former agricultural land the financial and bulk maturity age of silver birch has been found to vary in the range of 34–45 years (Tullus *et al.*, 2012a). During the rotation period, one to three thinnings are planned in hybrid aspen and silver birch plantations, except in plantations with very low initial planting density.

All the silver birch plantations in the study are one ha in size; the sizes of naturally regenerated stands vary from 0.5 to 2 ha. The sizes of hybrid aspen plantations vary from 0.7 to 32 ha, and 14 larger hybrid aspen plantations consist of smaller stands or parts with different soil type and land use history. Previous agricultural land use for plantations and naturally regenerated stands was either crop field or grassland (Table 1). In silver birch plantations whole-area ploughing was applied as a mechanical site preparation method before planting trees; in hybrid aspen plantations, besides whole-area ploughing, strip tillage was also used (Table 1). No chemical vegetation removal treatment was applied in the establishment phase. However, in the case of hybrid aspen, in areas with intensive grass growth, the grass was flattened by foot one or two times during the first season after planting.

Table 1. The distribution of the studied deciduous forest plantations and naturally regenerated stands according to overstorey tree species, previous land use and mechanical site preparation method.

Tree species	Previous land use	Site preparation method	Experimental plots	Vegetation plots
Hybrid aspen (planted)	Crop field	Whole-area ploughing	13	52
		Strip tillage	15	60
	Grassland	Whole-area ploughing	5	20
		Strip tillage	18	82
Silver birch (planted)	Crop field	Whole-area ploughing	6	24
	Grassland	Whole-area ploughing	5	20
Birch (naturally regenerated)	Crop field	-	3	12
	Grassland	-	8	32

4.2. Data collection

Floristic data were collected from 7 to 9-year-old hybrid aspen and silver birch plantations (the first monitoring). Silver birch plantations were remonitored at the age of 13 years and hybrid aspen plantations at the age of 13–14 years (the second monitoring). The age of naturally regenerated stands at the time of data collection varied approximately from 14 to 20 years. Field works were carried out in July of the years 2005, 2006, 2007, 2011 and 2012.

As a basis for data collection, 73 long-term experimental plots created previously for studying and monitoring the growth dynamics and productivity of birches and aspens at various site conditions (Vares, 2005; Tullus, 2010) were used. The size of an experimental plot was 0.1 ha; 11 experimental plots had been created in silver birch plantations, 11 in naturally regenerated birch stands and 51 in hybrid aspen plantations. In 73 experimental plots 292 permanent vegetation plots (each 2 × 2 m in size, four in each experimental plot) were established for the characterization of understorey vegetation. Four vegetation plots were distributed systematically across each 0.1 ha experimental plot, with two vegetation plots on both sides of the experimental plot centre. In every vegetation plot a list of vascular plant and bryophyte species was compiled. The total percentage cover of the field and bryophyte layers and the percentage cover of individual species were estimated. In 7 to 9-year-old hybrid aspen and silver birch plantations no bryophytes were found growing on the trunks of trees. By the time of the second monitoring, bryophytes were growing also on tree bases and trunks and for every vegetation plot a list of bryophyte species growing on the trunks of four trees situated near the vegetation plot corners was compiled. Bryophytes that could not be identified in field conditions were collected for further investigation under the microscope. The nomenclature follows the keybooks of Estonian vascular plants (Leht, 1999) and bryophytes (Ingerpuu and Vellak, 1998).

In order to study relations between the understorey vegetation and the tree layer, several overstorey characteristics were measured. At the time of the first monitoring the canopy diameter of all the trees within experimental plots was measured in hybrid aspen plantations and the percentage canopy cover was estimated. As the canopies had not closed, it was computed as the ratio of the sum of circular crown projections of individual trees to the area of experimental plot. In addition, stem diameter at breast height (DBH) of all the trees within the experimental plots was measured and stand basal area (BA) per hectare was estimated in all stands. In naturally regenerated stands and at the time of second monitoring in plantations hemispherical (fisheye) photos were taken from the centre of each vegetation plot of the understorey vegetation layer (from a height of approximately 50 cm) using a Sigma 8 mm 1:3.5 EX DG FISHEYE lens attached to a Canon EOS 5D digital camera. The photos were analysed with Gap Light Analyzer 2.0 (Frazer *et al.*, 1999) to estimate canopy openness and the amount of below-canopy (transmitted) direct, diffuse, and total solar radiation incident on a horizontal receiving surface.

At the time of the first monitoring, a soil sample was taken from the middle part of the humus horizon at the centre of each vegetation plot, from which pH_{KCl} and concentrations of total nitrogen (N) and extractable phophorus (P) and potassium (K) were determined. Analyses were performed by the Laboratory of Agrochemistry of the Agricultural Research Centre in Saku. The total N in soil samples was determined by the Kjeldahl procedure (method ISO 11261). To analyse available P and K in the soil, Mehlich 3 extractant was used. The soil pH in 1M KCl suspensions was measured in the ratio 10 g : 25 ml (method ISO 10390). The experimental plots were grouped according to soil moisture conditions, based on earlier studies (Jõgiste *et al.*, 2003, Tullus *et al.*, 2007).

At the time of the second monitoring, leaf and branch litter samples were additionally collected. Leaf and branch litter was collected from two subplots (each 20 × 20 cm) located at opposite sides of a vegetation plot. From the same subplots, soil samples were taken from the middle of the humus horizon. Composite samples of litter and soil from each vegetation plot were taken for laboratory analyses. Litter samples were dried at +70 ºC to constant weight and weighed to the nearest 0.001 g. Dry litter mass estimates (t ha^{-1}) were then calculated for each vegetation plot. Soil analyses were performed by the same laboratory using the same methods as were used for the first monitoring.

Using the aerial photos provided by Estonian Land Board (http://xgis.maaamet.ee/xGIS/XGis), distance from experimental plot to the nearest forest was estimated for study **IV**.

4.3. Data analysis

Several floristic traits were used to characterize the vascular plants and bryophytes growing in the understorey of forest plantations. Ecological strategy types (competitors, competitors/ruderals, competitors/stress-tolerators, competitors/stress-tolerators/ruderals and ruderals) were assigned to vascular plant species according to Grime (2001) and life-span categories (annuals, biennials and perennials), according to Leht (1999). Based on the BIOFLOR database (Klotz *et al.*, 2002) and the Estonian keybook of vascular plants (Leht, 1999), species were classified by habitat preference into the following categories: forest species, grassland species, forest and grassland species, fallow species, grassland and fallow species. Ellenberg indicator values for light, moisture, pH and nitrogen were assigned to vascular plant species according to Lindacher (1995) and weighted average Ellenberg values were calculated for vegetation plots. Based on Kukk (1999), vascular plant species were grouped according to their sensitivity to human impact into the following categories: apophytes, hemeradiaphores and anthropophytes. The status of the species in the Estonian flora (native *versus* alien) was determined based on Kukk and Kull (2005). Based on the system of bryophyte life strategies (During, 1992), bryophyte species were classified into the following categories: species with a life span of a few years (pioneer colonists, colonists, short-lived shuttle) and species with a life span of many years (competitive perennials, perennials, stress tolerant perennials, long-lived shuttle) according to Dierßen (2001). Light value index was assigned to bryophyte species according to Düll (1991). Habitat and substrate preference of bryophyte species was determined based on Ingerpuu *et al.* (1994) and Ulvinen *et al.* (2002).

Species richness (S) and Simpson's diversity index (D') of vascular plants were estimated for vegetation plots with PCORD-4 (McCune and Mefford, 1999) as follows: species richness = n, Simpson's $D' = 1 - \Sigma(p^2_i)$, where n is the number of species present in the vegetation plot and p_i is the proportion of the sample belonging to the ith species. In study **III**, arithmetic mean species richness and coverage of the bryophyte layer were estimated for all experimental plots on the basis of vegetation plot-level measures of these variables. In addition, total bryophyte species richness of the experimental plot, number of species with a life span of a few years, and number of species with a life span of many years were estimated on the basis of all species found within four vegetation plots. In study **IV**, species richness and diversity of bryophytes growing on the ground, and species richness of bryophytes growing on the trunks of trees were recorded for all vegetation plots. In addition, on the basis of combined data of bryophytes growing on the ground and on tree trunks, species richness of bryophytes was estimated for all vegetation plots.

Detrended Correspondence Analysis (DCA) and Non-metric Multidimensional Scaling (NMDS) were used for ordination of floristic data. DCA was performed with PCORD-4, and NMDS with the community ecology package Vegan 1.15-1 for R (Oksanen *et al.*, 2008). Species with less than two occurrences were excluded and vascular plant and bryophyte data were analysed separately. To interpret the ordination axes, Spearman rank correlations between DCA plot scores and soil variables were calculated. The Kruskall-Wallis test was used to test the significance between group means of DCA axis1 and axis2 scores followed by the Mann-Whitney test. In study **IV**, Spearman rank correlations were calculated between DCA axes scores and continuous site variables, and the effect of discrete factors on vegetation plot-level DCA scores was checked with the mixed model (SAS PROC MIXED), where experimental plot was treated as a random variable. In the case of NMDS (study **II**), environmental vectors and a factor were fitted onto the NMDS plot using the function 'envfit' (Oksanen *et al.*, 2008).

Differences between groups formed on the basis of previous agricultural land use, site preparation method and canopy cover were tested with Multiresponse Permutation Procedures (MRPP) using the Euclidean distance measure. The significance of differences in the frequency of occurrence of common vascular plant species (i.e. species present in at least 10% of the studied vegetation plots in hybrid aspen plantations) according to previous agricultural land use and site preparation groups was tested using SAS's PROC GENMOD, followed by estimate statement (chi-square test). The same method was used to test the significance of differences in the distribution of vascular plant species into ecological groups between hybrid aspen and silver birch plantations. In order to assess species' association with stand type (plantation or naturally regenerated stand) Indicator Species Analysis (Dufrêne and Legendre, 1997) was performed.

The normality of variables was checked with Shapiro-Wilk's and Kolmogorov-Smirnov tests; if necessary, log- or square-root-transformations of the variables were used. The t-test was used to test the differences in the group means of experimental-plot-level variables between silver birch and hybrid aspen plantations (**II**). In study **III** the t-test was applied to analyse the effect of tree layer species, previous agricultural land use, and site preparation method on experimental-plot-level estimates of bryophyte characteristics.

As data were hierarchical (containing both vegetation-plot and stand-experimental-plot-level estimates), mixed models (with experimental plot treated as a random effect) were applied in studies **I**, **II** and **IV** to evaluate the effect of environmental variables on the vegetation-plot-level characteristics. In studies **I** and **II**, PROC MIXED with SAS for Windows 9.1.3 was applied. The normality of the variables included to the model was checked and transformed if necessary. In study **IV**, a generalized linear model with SAS PROC GLIMMIX was applied. Species richness estimates were treated as response variables with Poisson distribution, while Gaussian distribution was used for coverage estimates and diversity indices. To evaluate the significance of the change in the vegetation characteristics between the first and the second monitoring in hybrid aspen and silver birch plantations, repeated measures analysis was applied.

The associations were considered to be significant when $p < 0.05$. Arithmetic means are presented with ± standard error in the text.

In the study characterizing the understorey vegetation of young hybrid aspen plantations (**I**), all experimental plots in hybrid aspen plantations were included and the data from the first monitoring were used.

In the study comparing the understorey vegetation in half-exotic hybrid aspen and native silver birch plantations (**II**), only plantations established on former crop fields where whole-area ploughing had been used for site preparation and with similar soil type were included, with the aim of reducing the heterogeneity of the study area. As a result, six silver birch and seven hybrid aspen plantations were included and the data on vascular plants gathered during the first monitoring were used.

In the study analysing the bryophyte vegetation (**III**), the data from all experimental plots in hybrid aspen and silver birch plantations on former agricultural land were included. The study is based on bryophyte data from the first monitoring.

For analysing understorey vegetation characteristics in silver birch plantations and naturally regenerated stands (**IV**), all silver birch plantations and all naturally regenerated birch stands were included. The study relies on the vascular plant and bryophyte data of the second monitoring.

5. RESULTS

5.1. The impact of site and stand characteristics on understorey vegetation in young plantations (I–IV)

5.1.1. Previous agricultural land use and site preparation method

DCA ordination of vascular plant data from 7 to 8-year-old hybrid aspen plantations revealed the influence of previous land use and site preparation method on the first two DCA axes (Figure 4 in **I**). MRPP analysis confirmed the significant impact of previous agricultural land use and site preparation method (Table 4 in **I**). The comparison of frequency of occurrence of common vascular plant species (e.g species present in at least 10% of all studied vegetation plots) from 7 to 8-year-old hybrid aspen plantations showed a higher share of annual or biennial plants in previous crop fields and on whole-area ploughed sites (Figure 5 in **I**). A similar trend occurred for ruderals. Typical species of former grasslands and strip-tilled sites were perennials, with the majority of these species being competitors. The same analysis was repeated with the vascular plant data from 13 to 14-year-old hybrid aspen plantations (Figure 2) and the results were similar.

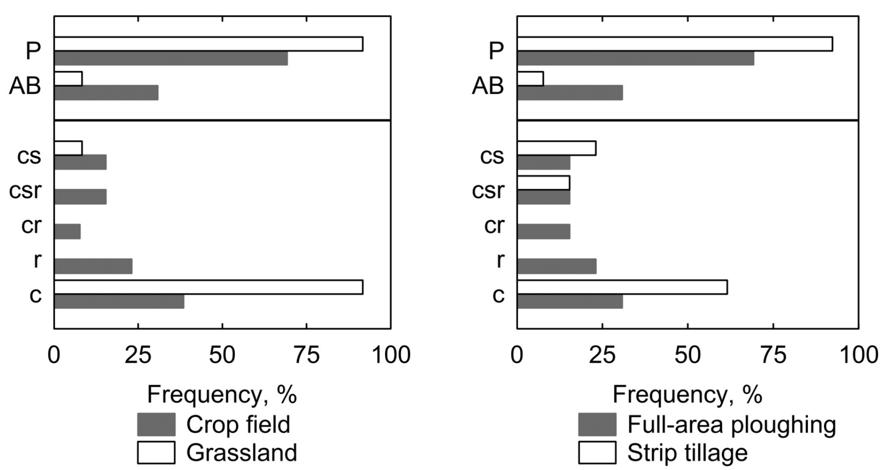

Figure 2. Life expectancy (AB: annuals and biennials, P: perennials) and Grime strategies (cs: competitors/stress-tolerators, csr: competitors/stress-tolerators/ ruderals, cr: competitors/ruderals, r: ruderals, c: competitors) of vascular plant species appearing significantly more frequently in sites with different former land use and site preparation history.

One hybrid aspen plantation can be singled out as a good example to illustrate the significant impact of former agricultural land use on species composition. Ahjametsa plantation was established in an area where *Galega orientalis* had been grown for fodder during the previous land use. Seven years later, at the time of the first monitoring, *G. orientalis* was a dominant species in the understorey, and the same was observed at the time of the second monitoring. Due to the dominance of *G. orientalis*, the mean number of vascular plant species per vegetation plot was the smallest among all the plantations at the time of both monitorings.

In the case of bryophytes, the number of species with a life span of a few years was significantly higher in 7 to 9-year-old hybrid aspen and silver birch plantations established on former fields and in the case of whole-area ploughed sites (Table 3 in **III**).

5.1.2. Soil properties and overstorey

The first two axes of DCA ordination of vascular plant data from the first monitoring of hybrid aspen plantations were correlated with soil moisture, pH_{KCl}, and concentrations of main mineral nutrients (NPK) in the humus horizon, while the influence of overstorey (canopy cover) was not detected (Figure 4 in **I**). Similarly, soil moisture, pH_{KCl} and concentrations of N and K significantly affected the positioning of the vegetation plots in the NMDS ordination diagram with vascular plant data from 7 to 9-year-old hybrid aspen and silver birch plantations, while overstorey (stand basal area) was significantly related to the understorey only in silver birch plantations, but not in hybrid aspen plantations (Figure 4 in **II**).

Soil pH_{KCl} was positively correlated with the cover of the bryophyte layer in 7 to 9-year-old hybrid aspen and silver birch plantations (Table 4 in **III**). In addition, the cover of the bryophyte layer was significantly higher in excessively well-drained soils (Figure 4 in **III**).

DCA ordination scores of vascular plant data from 13-year-old silver birch plantations and naturally regenerated birch stands correlated with soil nutrients and pH_{KCl}, stand basal area and leaf and branch litter characteristics, and distance to forest (Table 6 in **IV**). Bryophyte DCA scores of the same stands were significantly affected by overstorey stand growth (basal area, leaf and branch litter), transmitted solar radiation and soil pH_{KCl} and concentration of K (Table 6 in **IV**). The influence of previous agricultural land use on DCA ordination scores could not be detected in either of the cases (Table 5 in **IV**).

5.1.3. Factors affecting species richness

Site preparation method additionally influenced species richness and Simpsons's diversity index of vascular plants per vegetation plot in 7 to 8-year-old hybrid aspen plantations, as fewer species appeared in the areas where whole-area ploughing had been applied (Table 3 in **I**). On average 15.3±0.5 species were found in the vegetation plots of whole-area ploughed sites and 17.9±0.5 species in the vegetation plots of strip-tilled sites. Species richness of vascular plants was also correlated to the concentrations of major mineral nutrients in the humus horizon, as higher concentrations of NPK reduced the species richness. However, bryophyte vegetation of 7 to 9-year-old hybrid aspen and silver birch plantations did not show a similar response to site preparation method, as the species richness of bryophytes was similar in whole-area ploughed and strip-tilled sites (Table 3 in **III**).

By the time of the second monitoring, the effect of site preparation on vascular plant species richness had become insignificant in hybrid aspen plantations, with the change in species richness being significantly ($p = 0.02$) higher in whole-area ploughed sites, where the number of species per vegetation plot had increased on average by 4.4±0.5.

5.2. Understorey vegetation characteristics in semi-exotic hybrid-aspen and native silver birch plantations (II, III)

Due to different planting densities recommended for establishing hybrid aspen and silver birch plantations in Estonia the stand density of silver birch plantations was almost two times higher than stand density in hybrid aspen plantations at the age of 7 to 9 years (Table 2 in **II**). Nevertheless, the majority of the understorey vegetation characteristics were similar in hybrid aspen and silver birch plantations. Species richness and Simpson's diversity index of vascular plants, as well as the average number of bryophytes per vegetation plot did not differ between the two plantation types (Table 2 in **II**, Table 3 in **III**). Species richness of vascular plants and bryophytes, estimated on experimental plot level, were also similar (Table 2 in **II**, Table 3 in **III**). No significant differences were found in the distribution of vascular plant species into habitat preference, sensitivity to human impact, and life span groups between hybrid aspen and silver birch plantations. Both plantation types were dominated by species belonging to similar ecological groups (grassland species, apophytes, perennials) (Figure 3 in **II**); no alien vascular plant species were found in the understorey vegetation. The average total cover of the field layer did not differ between plantation types (Table 2 in **II**). In the majority of vegetation plots in both plantation types the total cover of the bryophyte layer was below 10%. However, a slightly higher share of vegetation plots with total cover of the bryophyte layer ranging from 10% to 30% was found in silver birch plantations (Figure 3b in **III**). As the main difference between hybrid aspen and silver birch plantations, a significantly higher share of shade tolerant species (with Ellenberg light value 3–6) was found in silver birch plantations and a higher share of half-light and light species (with Ellenberg light value 7–9) in hybrid aspen plantations (Table 2 in **II**).

5.3. The formation of forest understorey (I–IV)

5.3.1. Differences between the first and the second monitoring in hybrid aspen and silver birch plantations

Altogether 184 vascular plant species were identified in the vegetation plots in hybrid aspen and silver birch plantations at the time of the first monitoring. The respective number for the second monitoring was 197. Additionally, there were a few specimens that were identified on the genera level. The majority of species found from the vegetation plots in hybrid aspen and silver birch plantations were common species. As an exception, at the time of the first monitoring an orchid (*Platanthera sp*) grew in one hybrid aspen plantation. However, at the time of the second monitoring, orchids (*Dactylorhiza incarnata*, *D. fuchsii*, *Platanthera bifolia*) were found from the vegetation plots in six experimental plots in hybrid aspen plantations. When species found from experimental plots with a size of 0.1 ha were taken into account, orchids (genera *Dactylorhiza* and *Platanthera*) grew in 10 experimental plots in hybrid aspen plantations and *Epipactis helleborine* in one experimental plot in a silver birch plantation. *Thalictrum lucidum* (third category protected species) was found from one experimental plot in a hybrid aspen plantation.

The share of forest vascular plant species in the understorey of 7 to 9-year-old hybrid aspen and silver birch plantations was low and dominant species in the understorey were grassland species (Figure 3). The 10 vascular plant species found most frequently on the vegetation plots were all species typical to open communities (i.e grasslands, fallows) (Table 2).

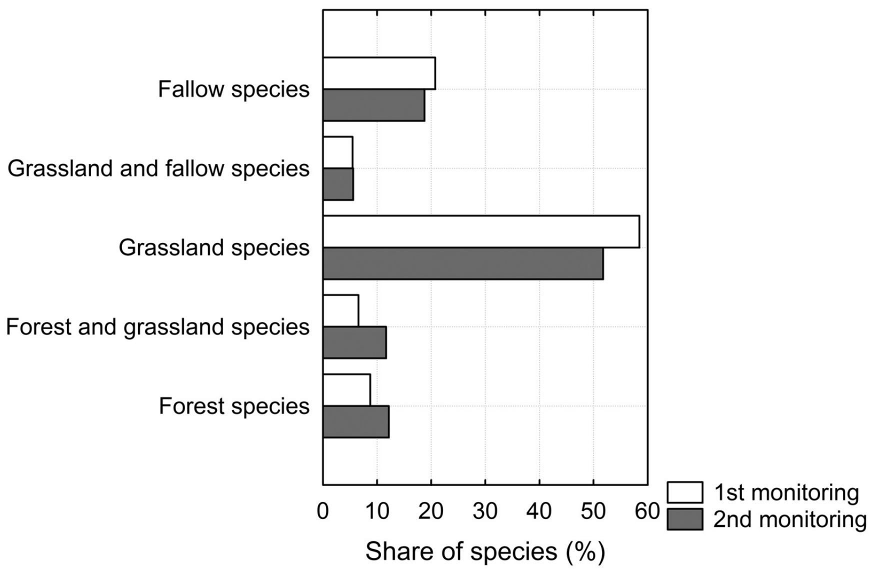

Figure 3. Distribution of all the vascular plant species found on the vegetation plots of hybrid aspen and silver birch plantations into habitat preference groups.

Table 2. Ten most frequently found vascular plant species in the vegetation plots of hybrid aspen and silver birch plantations.

First monitoring		Second monitoring	
Vascular plant species	Share of plots (%)	Vascular plant species	Share of plots (%)
Taraxacum officinale (coll.)	82	*Taraxacum officinale* (coll.)	77
Elymus repens	81	*Elymus repens*	71
Cirsium arvense	77	*Phleum pratense*	64
Phleum pratense	64	*Cirsium arvense*	63
Achillea millefolium	56	*Achillea millefolium*	52
Vicia cracca	50	*Equisetum arvense*	52
Artemisia vulgaris	49	*Anthriscus sylvestris*	51
Equisetum arvense	42	*Vicia cracca*	46
Agrostis capillaris	40	*Dactylis glomerata*	44
Cerastium fontanum subsp. *vulgare*	40	*Artemisia vulgaris*	42

Altogether 38 bryophyte species were found in 221 vegetation plots from hybrid aspen and silver birch plantations at the time of the first monitoring. In 27 vegetation plots the bryophyte layer was absent; neither were bryophytes found on the trunks of the trees. All observed bryophyte species were common. 45% of bryophytes found from the plantations were forest and grassland(field) species, 42% forest species and 13% species typical to open communities. The majority of bryophytes were light-demanding species (Figure 2 in **III**). On the basis of substrate preference, the majority of bryophyte species were either epigeic or generalists, growing on a variety of different substrata (Appendix in **III**).

By the time of the second monitoring (at the age of 13–14 years) all the plantations were still dominated by grassland species, followed by fallow species, forest species, forest and grassland species and grassland and fallow species (Figure 3). The 10 most frequently found vascular plant species were still species typical to open communities (Table 2). However, some differences had occurred between vegetation characteristics in hybrid aspen and silver birch plantations. The number and cover of forest species and the number and cover of forest and grassland species per vegetation plot had significantly increased in hybrid aspen plantations (Table 3). A similar, although statistically insignificant, increase was observed in silver birch plantations as well. The number of grassland species had increased in hybrid aspen plantations but decreased in silver birch plantation. The cover of grassland species had decreased in both plantation types. The number of fallow species had significantly decreased only in silver birch plantations. The cover of fallow species was significantly smaller at the time of the second monitoring in both plantation types. The cover of the field layer had dropped in both plantations types, and the vegetation plot mean Ellenberg value for light had also decreased in both cases. Species richness of vascular plants per vegetation plot was higher at the time of the second monitoring in hybrid aspen plantations, while the opposite trend was observed in silver birch plantations.

Table 3. Vegetation plot mean values of vascular plant (VP) and bryophyte (B) characteristics at the time of the 1st monitoring (age 7–9 years) and the 2nd monitoring (age 13–14 years) in hybrid aspen and silver birch plantations. S=species richness, C=cover.

	Hybrid aspen plantations				Silver birch plantations			
	1st monitoring	2nd monitoring	Change	p-value	1st monitoring	2nd monitoring	Change	p-value
Vascular plants								
S_{VP}	16.7±0.4	19.5±0.4	2.7	**<0.001**	17.4±0.8	12.8±0.7	-4.5	**0.005**
C_{VP}	70.1±0.8	61.5±1.1	-8.6	**<0.001**	68.3±3.2	44.1±3.3	-24.2	**0.005**
Ellenberg value for light	7.0±0.02	6.8±0.03	-0.2	**<0.001**	7.0±0.1	6.6±0.1	-0.4	**0.002**
S_{VP_forest}	0.4±0.1	0.9±0.1	0.5	**<0.001**	0.7±0.2	1.0±0.2	0.3	0.147
$S_{VP\_forest, grassland}$	0.2±0.03	0.5±0.05	0.3	**<0.001**	0.6±0.2	0.9±0.2	0.2	0.117
$S_{VP\_grassland}$	10.3±0.3	12.1±0.3	1.8	**<0.001**	11.0±0.7	7.9±0.6	-3.1	**0.002**
$S_{VP\_grassland, fallow}$	1.2±0.1	1.2±0.1	-0.04	0.437	1.0±0.1	0.7±0.1	-0.3	0.065
S_{VP_fallow}	4.2±0.2	4.0±0.2	-0.2	0.470	3.9±0.4	2.3±0.3	-1.6	**0.009**
C_{VP_forest}	0.8±0.1	3.6±0.7	2.8	**0.001**	1.1±0.3	1.6±0.4	0.5	0.253
$C_{VP\_forest, grassland}$	1.1±0.3	4.6±0.8	3.5	**0.001**	6.3±2.3	9.8±3.3	3.5	0.318
$C_{VP\_grassland}$	50.4±1.5	40.1±1.3	-10.3	**<0.001**	45.5±2.7	25.7±2.6	-19.7	**0.003**
$C_{VP\_grassland, fallow}$	6.7±0.5	7.0±0.6	0.3	0.772	7.0±1.4	4.5±1.0	-2.5	0.085
C_{VP_fallow}	17.4±1.3	12.3±0.9	-5.1	**0.004**	17.7±3.0	7.5±1.6	-10.1	**0.033**
Bryophytes								
C_{B}	11.7±1.5	22.8±1.7	11.1	**<0.001**	10.7±2.6	4.7±0.9	-6.0	0.158
S_{B_ground}	1.8±0.1	3.7±0.2	1.8	**<0.001**	1.9±0.4	2.0±0.3	0.02	0.948
S_{B_trunk}	-	2.3±0.1			-	1.4±0.4		

At the time of the second monitoring altogether 60 bryophyte species were found growing on 244 vegetation plots and on the trunks of the bordering trees in silver birch and hybrid aspen plantations. In four vegetation plots the bryophyte layer was absent. In 34 cases, bryophytes were not found from the trunks of the trees. The share of forest species among the bryophytes found from the plantations had increased to 52% and the share of forest and grassland (field) species had declined to 30%, while the share of species typical to open communities had remained at the same level compared to the first monitoring (13%). Additionally, 5% of the bryophyte species were species that usually grow on tree trunks. The cover of the bryophyte layer and the species richness of bryophytes had increased in the case of hybrid aspens, while no significant change was observed in silver birch plantations (Table 3).

Due to the significantly higher density of silver birch plantations, the mean basal area was also higher in silver birch plantations at the time of the second monitoring (Table 4). Canopy openness and the amount of transmitted solar radiation were significantly higher in hybrid aspen plantations.

Table 4. Comparison of tree layer characteristics and light conditions for the understorey in silver birch and hybrid aspen plantations at the time of the second monitoring. BA=stand basal area, DBH=diameter at breast height.

Variable	Silver birch	Hybrid aspen	t-value	p-value
Estimated for each experimental plot (t-test):				
Trees (ha^{-1})	1883±164	1017±27	9.24	**<0.001**
BA (m^2 ha^{-1})	12.20±1.39	8.90±0.59	2.33	**0.023**
DBH (cm)	8.60±0.63	10.19±0.35	-1.94	0.057
Estimated for each vegetation plot (mixed model):				
Canopy openness (%)	13.95±2.28	22.26±0.87	-2.15	**0.036**
Transmitted solar radiation:				
Direct (mol m^{-2} d^{-1})	1.56±0.29	3.26±0.15	-2.86	**0.006**
Diffuse (mol m^{-2} d^{-1})	2.12±0.31	3.76±0.13	-2.93	**0.005**
Total (mol m^{-2} d^{-1})	3.68±0.60	7.02±0.27	-2.92	**0.005**

5.3.2. Factors affecting the formation of forest understorey

In the study comparing silver birch plantations and naturally regenerated birch stands, former agricultural land use, soil properties, distance to nearest forest, leaf and branch litter, transmitted total radiation and stand basal area were included as possible factors affecting the formation of the forest understorey. The impact of former agricultural land use on the occurrence of forest species was not detected, since a higher occurrence of forest species in former grasslands, due to the possible survival of forest species in reduced populations in former pastures and meadows, was not observed (Table 4 in **IV**). The influence of soil properties, leaf and branch litter, transmitted total radiation and stand basal area on the number of forest species could not be established either. However, the number of vascular plant species that usually grow in forests as well as in grasslands was affected by distance to nearest forest.

5.4. Forest plantations *versus* naturally regenerated stands (IV)

5.4.1. Stand and site characteristics

Soil characteristics (concentrations of main mineral nutrients and pH_{KCl} of the soil humus horizon) did not differ between naturally regenerated and planted birch stands (Table 2 in **IV**). The average amount of leaf litter was also similar in both stand types, whereas the amount of branch litter and thinning residues was three times higher in natural stands compared to plantations, where no thinnings had been carried out, with one exception. The mean diameter of birch trees was larger in plantations, but as natural stands were significantly denser, then there were no differences in the basal area and volume of the birch layer. Total basal area was higher in natural stands due to the second layer, which was formed mainly by *Picea abies* in the majority of natural stands. Light conditions of the understorey were similar in both stand types.

5.4.2. Understorey vegetation characteristics

Axis 1 of DCA ordination with vascular plant data, as well as with bryophyte data, separated silver birch plantations and naturally regenerated birch stands (Table 5 and Figures 2 and 3 in **IV**). Species richness and Simpson's diversity index of vascular plants per vegetation plot, as well as the mean number of vascular plant species in one stand (based on four vegetation plots), were similar in plantations and natural stands (Tables 3 and 4 in **IV**). Species richness and diversity of bryophytes growing on the ground per vegetation plot and the mean number of bryophyte species in a stand were significantly higher in naturally regenerated stands, while the number of bryophytes growing on the trunks of trees did not differ between plantations and naturally regenerated stands (Tables 3 and 4 in **IV**). The number of forest vascular plant species and the number of forest bryophyte species were significantly higher in naturally regenerated stands (Table 4 in **IV**). Indicator Species Analysis pointed to 11 vascular plant species characteristic to silver birch plantations and 8 vascular plant and 5 bryophyte species characteristic to naturally regenerated birch stands (Table 7 in **IV**). Species characteristic to plantations were all grassland or fallow species. The majority of the vascular plant species characteristic to naturally regenerated stands were forest or forest and grassland species and all characteristic bryophyte species were forest species.

6. DISCUSSION

6.1. The impact of site and stand characteristics on understorey vegetation in young plantations

The observable trends in the vegetation cover of 7 to 8-year-old hybrid aspen plantations were mostly driven by the disturbances that took place before the establishment of the plantations (previous agricultural land use and site preparation method), confirming the first hypotheses. The impact of these factors was revealed from DCA ordination, MRPP analysis, and from the analysis of the occurrence of common vascular plant species. According to DCA ordination, variation in vascular plant understorey vegetation was correlated with soil moisture, pH_{KCl} and concentrations of NPK in the humus horizon, but not with the overstorey (Figure 4 in **I**). This was not suprising in young and sparsely spaced plantations where canopy closure had only just begun, since the understorey is likely to respond to changes in the light availability with some delay (Brockerhoff *et al.*, 2003). Overstorey impact on understorey vegetation characteristics was revealed only in almost two times denser silver birch plantations at the time of the first monitoring (Figure 4 in **II**), as well as at the time of the second monitoring (Table 6 in **IV**). The impact of previous agricultural land use on DCA ordination scores with vascular plant and bryophyte data from naturally regenerated and planted birch stands could not be detected (Table 5 in **IV**), indicating that increasing overstorey impact could reduce the influence of former disturbances such as previous agricultural land use.

The results of studies **III** and **IV** highlighted the importance of soil pH for the bryophyte layer. This is in accordance with the other studies in the temperate zone, which have shown that soil pH affects significantly the distribution of bryophytes on grasslands (Virtanen *et al.*, 2000; Löbel *et al.*, 2006).

Species richness and Simpson's diversity index of vascular plants per vegetation plot in 7 to 8-year-old hybrid aspen plantations were influenced by site preparation method and concentrations of major minerals (Table 3 in **I**). Higher nutrient concentrations in the humus horizon significantly reduced species richness and diversity, referring to a trend observed in several fertilization experiments (e.g. Wilson and

Tilman, 2002; Hejcman *et al.*, 2007). Species richness of vascular plants was higher in the sites where strip tillage had been applied. Additionally there were no ruderals among the species typical of strip-tilled sites. Less intensive site preparation treatments tend to favour existing species, whereas more intensive treatments that destroy or remove the existing vegetation and vegetative reproductive structures tend to favour ruderal and invasive species (Haeussler *et al.*, 2002). Strip tillage allowed the vascular plant cover that had developed after the cessation of agricultual land use to survive in the 3–4 m gaps between furrows, whereas the ploughed strips allowed the colonization of new species. However, the same effect of site preparation method on species richness was not detected in the case of bryophytes, which were usually represented by only one to three species per vegetation plot (Figure 3 in **III**). By the time of the second monitoring the effect of site preparation method on the species richness of vascular plants was no longer perceivable in hybrid aspen plantations. New species additions to the vegetation plots included grassland, forest as well as forest and grassland species (Table 3). More new species were added to whole-area ploughed sites, and thus the impact of pre-establishment disturbance, via site preparation, on species richness could no longer be detected. However, for the species composition of vascular plants this effect had persisted (Figure 2).

6.2. Understorey vegetation characteristics in semi-exotic hybrid aspen and native silver birch plantations

As hypothesized, the majority of the studied understorey vegetation characteristics were similar in 7 to 9-year-old hybrid aspen and silver birch plantations indicating that although hybrid aspen is a semi-exotic tree species it provides similar habitat for the understorey as the native tree species silver birch. To reduce the heterogeneity of the study area only selected plantations (e.g. plantations established on former crop fields with similar soil type and the same site preparation method) were included to the study of vascular plant characteristics (**II**). No invasive alien plant species were found from the understorey of these plantations. However, in Ahjametsa hybrid aspen plantation, which was not included in study **II**, an invasive alien species *Galega orientalis* was a dominant in the understorey, allowing the growth of only a few other understorey vascular plant species. In this plantation the spread of *G. orientalis* arose from the former land use. As sparsely spaced hybrid aspens did not outcompete *G. orientalis* within 13 years, areas with similar land use history should be avoided in the future for the establishment of new forest plantations.

Another threat connected with the establishment of plantations with exotic species is a possible gene flow between exotic and native species, which poses a potential risk to biodiversity (Simberloff, 2008). Suvanto and Pulkkinen (2004) have shown that hybrid aspen can cross with European aspen and give viable seed. As *P. tremula* and *P. tremuloides* are genetically very similar, such development does not necessarily have harmful consequences (Tullus *et al.*, 2012b). In practice the risk of gene flow is also reduced due to the different flowering times of hybrid aspen and European aspen (Yu *et al.*, 2001). Mass propagation of new or until now less important pests and diseases in hybrid aspen plantations is also possible (Kasanen *et al.*, 2002). However, so far the spread of such pests and diseases have not been recorded in Estonian hybrid aspen plantations.

Bryophyte vegetation characteristics were similar in 7 to 9-year-old hybrid aspen and silver birch plantations (**III**). The cover of the bryophyte layer was low in both plantation types, coinciding with the trend observed also in hybrid poplar plantations in NE Germany (Zerbe, 2003) and in birch plantations in Latvia (Rūsiņa *et al.*, 2011). As the majority of bryophyte species were either epigeic or generalist, the silvicultural management of the plantations in the future should aim to provide new habitats for specialist bryophyte species (e.g. epixylic and epiphytic species). Leaving less-valuable residues on site during thinnings and keeping some retention trees after final harvest would probably be beneficial for bryophyte diversity in plantation forestry systems.

6.3. The formation of forest understorey in plantations on former agricultural land

Numerous studies have concluded that the vascular plant understorey of first generation forests developed on former agricultural land differs from typical forest understorey vegetation (Hermy, 1994; Petersen, 1994; Graae and Sunde, 2000; Singleton *et al.*, 2001; Bellemare *et al.*, 2002; Flinn and Vellend, 2005; Flinn and Marks, 2007; Hermy and Verheyen, 2007). The dominance of generalists or ruderals and the scanty occurrence of species typical of native deciduous forests in the understorey of fast-growing poplar plantations was observed in Sweden (Weih *et al.*, 2003) and in Germany (Heilmann *et al.*, 1995; Zerbe, 2003). Comparatively slow changes in the ground vegetation towards a forest understorey were observed also in Latvian forest plantations situated on former agricultural land (Rūsiņa *et al.*, 2011). According to Baum *et al.* (2012a), short rotation coppice plantations in Germany and Sweden were dominated by grassland species, followed by ruderal and woodland species; an increase in woodland species proportion and a decrease in grassland species proportion were dependent on tree cover and plantation age. Similarly to the referred studies, the proportion of vascular plant forest species was low in the understorey of young hybrid aspen and silver birch plantations in Estonia (Figure 3), confirming the third hypothesis. In addition, the proportion of light-demanding bryophyte species was high in the understorey of young plantations (**III**). Although the number and cover of vascular plant forest, and forest and grassland species slowly increased between the first and the second monitoring, the clear dominance of grassland species continued (Table 3), showing their high inertness and durability. Due to low planting density and the death of some trees as a result of damage by herbivores, the light conditions for the understorey were good in hybrid aspen plantations, facilitating the persistence of grassland species. The number of grassland species per vegetation plot even increased between the first and the second monitoring, although the cover of grassland species per vegetation plot decreased (Table 3). By the time of the second monitoring, hybrid aspen plantations had reached approximately half of the predicted rotation period. During the second monitoring, rapid dying of lower canopy branches was observed in hybrid aspen plantations. Therefore plenty of transmitted solar radiation still reached the understorey (Table 4) and it is reasonable to assume that the dominance of vascular plant species typical to open communities will continue through the years preceding the clear-cut. Generally, clear-cutting favours the spread of shade-intolerant early successional species (Yorks *et al.*, 2000) and changes are likely to occur in the understorey vegetation characteristics after harvest. However, in the second generation plantation, new hybrid aspen trees are expected to grow from root and stump suckers that may result in a very dense stand, consequently diminishing the light conditions for the understorey. For example, the mean density of suckers per hectare was 68056 two years after harvest in a hybrid aspen stand in Estonia (Lutter *et* *al.*, 2012) and 76000 in a hybrid aspen stand in southern Sweden (Rytter, 2006). In regenerating hybrid aspen stands different management schemes can be used aimed at producing energy wood in repeated very short rotations (less than five years) or at producing larger assortments during 20–30 years, similarly to the first generation (Tullus *et al.*, 2012b). Thus the conditions for understorey vegetation development could be substantially different in second generation hybrid aspen plantations, depending on the management scheme.

As the share of forest vascular plant and bryophyte species in the understorey of young hybrid aspen plantations was low, it may be concluded that young hybrid aspen plantations do no help to preserve flora typical of native deciduous forests. On the other hand, forests of European aspen are associated with high vascular plant species richness (Degteva, 2005) and aspen trees provide habitat for a unique epiphytic flora of bryophytes and lichens (Kuusinen, 1996). However, the high biodiversity of aspen forests is usually related to old, economically over-mature stands. Thus, shifting biomass production pressure onto short-rotation hybrid aspen plantations can help to reduce felling in old aspen forests and can help to preserve the related environmental values. At the same time, forest plantations on former agricultural land have been found to increase the floristic diversity of areas dominated by agriculture (Weih *et al.*, 2003) and to contribute positively to phytodiversity in rural landscapes with low habitat type heterogeneity (Baum *et al.*, 2012a; Baum *et al.*, 2012b). Another positive aspect of young hybrid aspen plantations is that they can provide habitat for species that need protection, such as orchids. The mass occurrence of orchids was recorded in poplar plantations established on abandoned agricultural land in Poland (Adamowski and Conti, 1991), where the extensive spread of *Dactylorhiza incarnata*, *Epipactis helleborine*, *Platanthera bifolia* suggested that poplar plantations may be suitable habitat for the mentioned orchid species. In Estonian hybrid aspen plantations orchids were found occasionally and further studies are needed to monitor the growth of orchids in the plantations in the future.

At the time of the first monitoring, a significantly higher share of shade tolerant species was found on the vegetation plots in silver birch plantations and a higher share of half-light and light species on the vegetation plots in hybrid aspen plantations, indicating the faster vegetation succession in denser silver birch plantations (Table 2 in **II**). During the second monitoring, transmitted solar radiation was evaluated with fish-eye photos in both plantation types. Percentage canopy openness was significantly smaller in silver birch plantations, and less canopy transmitted solar radiation reached the understorey of silver birch plantations (Table 4). The average numbers of forest, and forest and grassland species per vegetation plot were small in both plantation types at the time of the second monitoring (Table 3). However, the predicted rotation period for silver birch is longer than for hybrid aspen. Delaying plantation harvest is seen as one way to increase the number of forest plants in the understorey (Archaux *et al.*, 2010). Therefore, a longer rotation period may result in a higher share of forest species in the understorey of silver birch plantations by the time felling age is reached. On the other hand, denser silver birch plantations need to be thinned, which disturbs the ground vegetation.

As expected, the cover of the bryophyte layer increased between the first and the second monitoring in hybrid aspen plantations. Suprisingly, the same was not found in silver birch plantations. In Hiiumaa silver birch plantation, above average bryophyte cover values per vegetation plot were observed at the first monitoring (average bryophyte cover of four vegetation plots was 53%), but the cover had dropped remarkably by the time of the second monitoring (10%). Based on visual observation it was caused mainly by the accumulation of a thick *Festuca rubra* litter layer. A thick and persistent herb layer litter can have a negative effect on the bryophyte layer (Bartels and Chen, 2012).

The influence of former agricultural land use, soil properties, distance to nearest forest, leaf and branch litter, transmitted total radiation, and stand basal area on the formation of forest understorey was analysed in study **IV**. However, an impact was detected only in the case of distance to nearest forest, since the number of vascular plants that usually grow in forests as well as in grasslands in the vegetation plots of new forests was correlated to distance from nearest forest. The importance of distance from propagule sources for the recovery of the forest understorey has been emphazised in several studies (e.g. Dzwonko, 1993, 2001; Brunet *et al.*, 2000; Graae *et al.*, 2003). Contrary to Wulf (2004), higher occurrence of numerous forest species was not found in former grasslands, indicating that in the case of Estonian agricultural sites abandoned in the 1990s the formation of forest understorey occurs similarly in former fields and in former grasslands. Correlation between soil properties and the occurrence of forest species per vegetation plot could not be established either, indicating that soil properties do not limit the colonization of forest species to new forests at abandoned agricultural sites. This is in accordance with the results from Graae *et al.* (2004), who concluded, based on a seed sowing experiment, that soil variables did not influence the colonization of forest species to recent forests in Denmark.

6.4. Forest plantations *versus* naturally regenerated stands

One of the major fears with the establishment of forest plantations is that they develop into much less diverse associations compared to natural forests. Studies compiled in former mining sites have shown that naturally regenerated stands support higher species richness and more valuable species composition (Hodačova and Prach 2003; Pensa *et al.*, 2004; Tropek *et al.*, 2010; Prach *et al.*, 2011), while stand growth and yield characteristics may be better in plantations (Pensa *et al.*, 2004). Results from silver birch plantations and naturally regenerated birch stands on former agricultural lands (**IV**) confirm this view only partially. Stand growth parameters were not considerably better in plantations, as basal area and stand volume of birches were similar in planted and naturally regenerated stands, however, stem diameter at breast height of birches was larger in plantations (Table 2 in **IV**). Species richness and diversity of bryophytes were higher in naturally regenerated stands, confirming the hypothesis, but the species richness and diversity of vascular plants did not differ between the two stand types (Tables 3 and 4 in **IV**). Nevertheless, compositional differences were observed between planted and naturally regenerated stands, since the field layer of naturally regenerated stands contained a higher number of forest species than plantations, and as several forest, and forest and grassland species were characteristic to natural stands (Tables 4 and 7 in **IV**). The formation of the forest understorey had progressed further in naturally regenerated stands due to the longer succession and colonization period. While whole-area ploughing was applied as a method of site preparation before planting trees in plantations, no such disturbance took place in naturally regenerated stands and the colonization of forest understorey species to naturally regenerated stands could start simultaneously with birches after the cessation of agricultural land use. A similar conclusion was reached in the study of Canadian plantations and naturally regenerated stands growing on former agricultural lands (Aubin *et al.*, 2008), where the understorey of plantations was generally less developed than the understorey of naturally regenerated stands, due to the intensive site preparation method used in plantations.

In the case of bryophytes the compositional differences observed between two stand types were also supported by a significantly higher amount of branch litter and thinning residues in naturally regenerated stands (Table 2 in **IV**), which provided additional substrata for the bryophytes.

As stand growth parameters were not considerably better in plantations and a clear trend towards more diverse understorey vegetation was not observed in naturally regenerated stands in the case of vascular plants, both natural and artificial regeneration can be recommended as possible alternatives for the establishment of new birch forests on former agricultural lands. When the aim is to establish a commercial birch forest on abandoned agricultural land, both natural succession as well as plantation establishment are possible alternatives and they offer quite similar conditions for understorey vegetation. When the aim is to facilitate the restoration of a forest ecosystem then, for areas close to natural forests, natural succession can be recommended, which should result in a mixed stand, where colonization with forest understorey species is quite fast.

Another important aspect to consider is the difference in value and impact of plantations and natural stands on the landscape. In Estonia, only a few forest plantations with uniform shape and design have been established and they rather enrich the landscape. In countries where most forest stands are man-made and regularly managed, public opinion clearly favours natural-looking forests. In Estonia, half of forests are first-generation forests and less than 10% of them have been established as plantations. Natural regeneration of the main tree species as well as other tree species usually occurs in these forests during stand development (Tullus, 2009). To summarise, similarly with other Baltic and Nordic countries, Estonian forests are mainly semi-natural, differently from e.g. Denmark, Belgium or Ireland, where the share of forest plantations is very high (Relve, 2012). Public opinion would probably tolerate a certain increase in the area of forest plantations here.

6.5. Future prospects

The current study was planned as part of a long-term research program. Repeated descriptions of understorey vegetation are planned throughout the first rotation period in hybrid aspen plantations with the aim of clarifying whether the understorey of SRF plantations stays different from the understorey of native deciduous forest in the long run. Earlier studies (Halpern and Spiess, 1995; Weih *et al.*, 2003) have shown that repeated short-rotation harvests may reduce populations of many forest species, therefore the monitoring of understorey after clear-cut is also necessary. In addition to the vascular plants and bryophytes, also fauna, soil biota, insects, lichens and fungi need to be studied in SRF plantations.

In the silver birch plantations and naturally regenerated birch stands the monitoring of vegetation dynamics after thinnings is planned, with the aim of giving recommendations favourable to floristic diversity.

7. CONCLUSIONS

The observable trends in the understorey vegetation of young plantations were mostly driven by the former agricultural land use, site preparation method, and soil properties (pH_{KCl}, concentrations of main mineral nutrients, soil humidity). The species composition of 7 to 8-year-old hybrid aspen plantations was related to previous land use and site preparation method, since short-living ruderals were typical species to previous crop fields and whole-area ploughed sites (**I**). Similarly, the number of bryophyte species with a life span of a few years was significantly higher in hybrid aspen and silver birch plantations established on former fields and in the case of whole-area ploughed sites (**III**). In addition, site preparation method together with the concentrations of major mineral nutrients in the humus horizon impacted vascular plant species richness and diversity per vegetation plot in hybrid aspen plantations at the time of the first monitoring (**I**). However, by the time of the second monitoring, the effect of site preparation method on species richness was no longer perceivable. With increasing stand age the influence of pre-establishment disturbances becomes less pronounced and the impact of overstorey-related factors (basal area, leaf and branch litter, transmitted solar radiation) increases, as revealed from the study of planted and naturally regenerated birch stands (**IV**).

The majority of the vascular plant and bryophyte understorey vegetation characteristics were similar in young hybrid aspen and silver birch plantations (**II**, **III**) and it may be concluded that semi-exotic hybrid aspen provides similar habitat for understorey as native silver birch. According to previous experience, forest plantations can be established in Estonia without considerable risks of creating favourable habitat for new or previously introduced plant species, contrary to the situation in some other world regions. However, the establishment of plantations in the areas where invasive alien species (e.g *Galega orientalis*) are already present should be avoided in the future to avoid impoverished understorey vegetation and the persistence of alien species.

As hypothesized, the proportion of forest species was low in the vascular plant understorey of hybrid aspen and silver birch plantations at the time of both monitorings. Although the number and cover of forest species slowly increased between the two monitorings, clear dominance of grassland species continued at the age of 13 to 14 years.

As plenty of transmitted solar radiation reached the understorey of hybrid aspen plantations at the age of 13 to 14 years and the predicted rotation period is 20 to 30 years, the dominance of vascular plant species typical to open communities is likely to continue through the years preceding the clear-cut. In comparison with hybrid aspen plantations, significantly less transmitted solar radiation reached the understorey of silver birch plantations of the same age. At the same time the predicted rotation period for silver birch is longer than for hybrid aspen. These circumstances may facilitate the suppressing of grassland species and lead to a higher proportion of forest species in the understorey of silver birch plantations by the time of clear-cut.

The cover of the bryophyte layer was low in young plantations (**III**). Typical bryophytes were light-demanding perennials. Since the majority of bryophyte species were either epigeic or generalist, the silvicultural management of plantations in the future should include measures that provide habitats for epixylic and epiphytic species (e.g leaving some thinning residues on site and keeping retention trees after final harvest).

The hypothesis concerning higher understorey species richness of naturally regenerated stands in comparison with plantations was confirmed only partially as the species richness and diversity of bryophytes were higher in naturally regenerated birch stands, but the species richness and diversity of vascular plants did not differ between the two stand types (**IV**). However, significantly higher numbers of forest species (both vascular plant and bryophyte) indicated that the formation of forest understorey had progressed further in naturally regenerated stands. This can be explained by the longer undisturbed colonization period of naturally regenerated stands, since the colonization of forest understorey species could start simultaneously with birches, and the understorey was not disturbed by ploughing as it was in plantations. Both natural and artificial regeneration can be recommended as possible alternatives for the establishment of new forests on former agricultural land.

The view that afforestations on former grasslands may contain a higher number of forest species than afforestations on former fields was not confirmed by the current study (**IV**). An impact of soil properties on the formation of the forest understorey was not detected either. However, the results of the current study showed the importance of distance to the nearest forest as a propagule source.

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SUMMARY IN ESTONIAN

ALUSTAIMESTIK JA SEDA MÕJUTAVAD TEGURID ENDISTEL PÕLLUMAJANDUSMAADEL KASVAVATES NOORTES LEHTPUUISTANDIKES

Sissejuhatus

Alates 1990. aastate algusest on Ida- ja Põhja-Euroopas vähenenud põllumajanduslik maakasutus ning samal ajal on kasvanud puidu kui taastuvenergiaallika ja puidutööstuse toorme nõudlus. See on kaasa toonud intensiivmeetodil, sh lühikese raieringiga majandatavate puuistandike pindala kasvu nendes piirkondades. Tootmisele suunatud istandikes ehk puupõldudel ei ole peamiseks eesmärgiks metsökosüsteemi kujundamine, vaid soovitakse saavutada maksimaalne puidu või mõne teise puudega seotud toorme produktsioon. Puupõldude pindala pidev kasv tõstatab aga küsimuse, milline on nende mõju looduslikule, sh floristilisele mitmekesisusele. Kuigi mitmed uurimused on püüdnud sellele küsimusele vastata, on uurimistulemused vastuolulised, sõltudes näiteks sellest, millega puupõllu floristilist mitmekesisust võrreldakse. Seejuures on alustaimestikku puudutavad uurimused sageli käsitlenud üksnes soontaimede liigirikkust, ent samblaid ja samblarinde kujunemist istandikes on üsna vähe uuritud.

Alates 1999. aastast on Eestis endistele põllumajandusmaadele rajatud u 700 ha puuistandikke poolvõõrliigi hübriidhaavaga, mida plaanitakse majandada lühikese 20–30-aastase raieringiga. Mujal maailmas on võõrpuuliikidega rajatud istandikes täheldatud mõnikord keskkonnakaitselisi probleeme nagu vaesunud elustikku, võõrliikide levikut alustaimestikus ning kahjulike putukate ja seente masspaljunemist. Eestis puuduvad varasemad põhjalikud uurimused, mis käsitleksid alustaimestiku kujunemist endistel põllumajandusmaadel kasvavates hübriidhaavaistandikes ning ka naaberriikides on seda teemat vähe uuritud.

Kohalikest lehtpuudest soovitatakse Eestis endiste põllumajandusmaade metsastamiseks eelkõige arukaske, ent kaasikud võivad endistele põllumajanduskõlvikutele tekkida ka looduslikult. Endiste karjäärialade metsastamisel on istandike ja looduslikult tekkinud puistute võrdlusel täheldatud, et looduslikult tekkinud puistute alustaimestik võib olla liigirikkam ja mitmekesisem kui istandikes. Endistel põllumajandusmaadel kasvavates lehtpuupuistutes ei ole Eestis teadaolevalt seni võrdlevat uurimistööd tehtud ning ka maailmast on teada üksnes mõned uuringud.

Kirjanduse andmetel võib endistele põllumajandusmaadele rajatud metsade, sh istandike alustaimestik jääda pikaks ajaks (mõnedel andmetel koguni sajanditeks) erinevaks põliste metsade alustaimestikust. Põllumajanduslik maakasutus mõjutab mullaomadusi ning seemnepanka, enamasti eeldab metsa alustaimestiku taastumine endisel põllumajandusmaal metsaliikide kolonisatsiooni lähiümbruse metsadest. Lisaks võib alustaimestiku kujunemist mõjutada ka eelnev põllumajanduslik maakasutusviis, näiteks kas maad kasutati põllu- või rohumaana. Istandikes sõltub alustaimestiku kujunemine ka majandamistegevustest, näiteks avaldab alustaimestikule mõju istandiku rajamisel rakendatud maapinna ettevalmistusviis, herbitsiidide ja väetiste kasutamine jms.

Lähtuvalt eespool toodust seati doktoritööle järgnevad eesmärgid:
1) analüüsida, millised kasvukoha ja puistu tunnused mõjutavad alustaimestiku karakteristikuid (liigilist koosseisu ja liigirikkust) endistel põllumajandusmaadel kasvavates noortes hübriidhaava- ja arukaseistandikes (**I–IV**); 2) hinnata, kas poolvõõrliigi hübriidhaava istandikud pakuvad alustaimestiku liikidele sarnaseid kasvutingimusi kodumaise puuliigi arukase istandikega (**II, III**); 3) iseloomustada samblarinde kujunemist ja sammalde liigilist koosseisu endistel põllumajandusmaadel kasvavates noortes lehtpuuistandikes (**III**); 4) iseloomustada metsa alustaimestiku kujunemist endistel põllumajandusmaadel kasvavates noortes esimese generatsiooni puistutes (**I–IV**); 5) võrrelda alustaimestiku karakteristikuid arukaseistandikes ja endistele põllumajandusmaadele looduslikult tekkinud kaasikutes (**IV**).
Doktoritöös püstitati järgnevad hüpoteesid: 1) noore lehtpuuistandiku alustaimestiku karakteristikud sõltuvad eelnevast põllumajanduslikust maakasutusest ja istandiku rajamisel rakendatud maapinna ettevalmistusviisist (**I, III**); 2) alustaimestiku karakteristikud on kodumaise arukase ja poolvõõrliigi hübriidhaava istandikes sarnased (**II, III**); 3) metsaliikide (nii soon- kui sammaltaimede) osakaal endistel põllumajandusmaadel kasvavate noorte istandike alustaimestikus on väike (**I–IV**); 4) endistele põllumajandusmaadele looduslikult tekkinud puistute alustaimestik on liigirikkam kui istandikes (**IV**).

Materjal ja metoodika

Alustaimestikku iseloomustav andmestik koguti kuuekümne kahelt 0,1 ha suuruselt puude kasvukäigu uurimiseks rajatud püsiproovitükilt, mis paiknesid 11 arukase- ja 24 hübriidhaavaistandikus. Igale proovitükile rajati neli 2 × 2 m püsiprooviruutu, mille kohta koostati soon- ja sammaltaimede nimekirjad koos liikide katvustega. Alustaimestiku kirjeldused tehti esimest korda 7–9-aastastes istandikes ning korduskirjeldused 13–14-aastastes istandikes. Lisaks koguti võrdlusandmeid endistele põllumajandusmaadele looduslikult tekkinud kaasikutest 11 proovitükilt, kus puurinde ligikaudne vanus oli 14–20 aastat. Igalt prooviruudult võeti huumushorisondist mullaproovid happesuse ja peamiste toitainete (NPK) sisalduse määramiseks, korduskirjelduste ajal koguti ka lehe- ja oksavarise proovid ning tehti kalasilmafotod alustaimestiku valgustingimuste kirjeldamiseks. Puurinde iseloomustamiseks arvutati iga prooviala kohta rinnaspindala, hübriidhaavikutes hinnati esimesel kirjeldusel ka puuvõrade katvus.

Alustaimestikus esinenud soontaimede liigid rühmitati kirjanduse alusel, kasutades erinevaid ökoloogilisi grupeeringuid: Grime'i strateegiad, eluiga, kasvukoht, kultuurisuhe, seisund flooras. Sammalde grupeerimisel võeti aluseks sammalde elustrateegiad ja kasvukoha ning substraadi eelistused. Soontaimede valgusnõudlikkuse iseloomustamiseks kasutati Ellenbergi väärtarve (Lindacher, 1995) ja sammaldel Dülli (1991) väärtarve.

Alustaimestiku võrdlemiseks erineva maakasutuse, maapinna ettevalmistusmeetodi ja puistutüübi alusel moodustatud rühmades ning kasvukohatunnuste mõju tuvastamiseks kasutati klassikalisi geobotaanilisi analüüsimeetodeid (DCA, NMDS, indikaatorliikide analüüs). Taimeruudu kohta arvutatud keskmiste karakteristikute ja ordinatsioonitelgede väärtuste hajuvust mõjutanud tegurite kindlakstegemiseks kasutati lineaarseid segamudeleid, mis arvestasid proovitükki juhusliku faktorina.

Tulemused ja järeldused

Endistele põllumajandusmaadele rajatud noore istandiku alustaimestiku karakteristikuid mõjutasid esialgu eelnev põllumajanduslik maakasutus, istandiku rajamisel rakendatud maapinna ettevalmistusviis ja mullastiku tingimused (mulla happesus, NPK-sisaldus ja mulla niiskus). Lühiealised ruderaalid olid tüüpilised liigid 7–8-aastastes hübriidhaavikutes, mis olid rajatud endistele põldudele või kus oli rakendatud istandiku rajamisel ülepinnalist kündi (**I**). Sellistes hübriidhaava- ja arukaseistandikes kasvas ka rohkem lühiealisi samblaliike (**III**). Maapinna ettevalmistusviis ja mulla peamiste toitainete (NPK) sisaldus mõjutasid soontaimede liigirikkust ja liigilist mitmekesisust hübriidhaavikute prooviruutudel (**I**). Kuid korduskirjeldusel ei ilmnenud enam maapinna ettevalmistusviisi mõju soontaimede liigirikkusele. Istandike vanuse kasvades muutub istandiku rajamisele eelnenud häiringute mõjust olulisemaks puurindega seotud tegurite (rinnaspindala, lehe- ja oksavarise, valgustingimuste) mõju rohu- ja samblarindele (**IV**).

Hübriidhaava- ja arukaseistandike alustaimestiku (soontaimede ja sammalde) karakteristikud olid suures osas sarnased (**II, III**). Seniste uurimistulemuste põhjal saab väita, et hübriidhaavikute rajamisega Eestis ei kaasne alustaimestikus ebasobivaid arenguid, nt võõrliikide levikut. Samas peaks vältima istandike rajamist aladele, kus invasiivne võõrliik on alustaimestikus dominandina esindatud varasema maakasutuse tõttu.

Metsaliikide osakaal hübriidhaava- ja arukaseistandike alustaimestikus oli väike nii esimese kirjelduse kui ka korduskirjelduse ajal (joonis 3). Hoolimata sellest, et metsaliikide arv ja katvus suurenesid vähehaaval, domineerisid ka 13–14-aastaste istandike alustaimestikus jätkuvalt rohumaaliigid (tabel 3). Kuna selles vanuses hübriidhaavikutes jõudis alustaimestikuni endiselt palju valgust (tabel 4) ja ennustatav raiering on keskmiselt 20–30 aastat, ei pruugi metsaliikide osakaal lageraiele eelneva ajaga oluliselt kasvada ning võib arvata, et esimese generatsiooni hübriidhaavikute alustaimestik jääbki kohalike lehtpuumetsade omast erinevaks. Võrreldes hübriidhaavikutega jõudis 13–14 aasta vanustes arukaseistandikes alustaimestikuni oluliselt vähem valgust, kuid ennustatav raiering on pikem. Need asjaolud võiksid soodustada avatud kasvukohtade liikide tugevamat allasurumist ja metsaliikide suuremat osakaalu raieringi lõpuks.

Samblarinde katvus noortes istandikes oli väike (**III**). Tüüpilised noortes istandikes kasvavad liigid olid valgusnõudlikud mitmeaastased samblad. Kuna enamik istandikest leitud liike olid kas epigeilised või liigid, mis võivad kasvada paljudel erinevatel substraatidel, oleks istandike edasisel majandamisel soovitatav rakendada abinõusid (osa raiejäätmete jätmine alale, säilikpuude jätmine), mis pakuvad lisakasvukohti epiksüülsetele ja epifüütsetele liikidele.

Hüpotees, et endistele põllumajandusmaadele looduslikult tekkinud puistud toetavad suuremat alustaimestiku liigirikkust, leidis kinnitust üksnes osaliselt (**IV**). Maapinnal kasvanud sammalde arv ja mitmekesisusindeks olid looduslike kaasikute prooviruutudel usaldusväärselt suuremad, ent soontaimede liikide arv ja mitmekesisusindeks olid arukase istandikes ja looduslikes kaasikutes sarnased. Looduslike kaasikute alustaimestikus kasvas aga rohkem metsaliike (nii soon- kui sammaltaimi). Seda võib seletada pikema rahuliku suktsessiooni ajaga, kuna looduslikes puistutes jäi ära istandiku rajamisega kaasnev ülepinnaline künd ja metsaliikide kolonisatsioon sai alata paralleelselt kase isekülviga. Lisaks oli looduslikes kaasikutes oluliselt rohkem oksavarist ja raiejäätmeid, mis pakkusid sammaldele lisasubstraate.

Kirjanduses on arvatud, et metsa alustaimestiku kujunemist endisel põllumajandusmaal võivad mõjutada mitmed tegurid, nagu mullastiku omadused ja eelnev põllumajanduslik maakasutus. Käesolevas doktoritöös selliseid seoseid ei leitud (**IV**). Kuid olulise tegurina võib välja tuua kauguse metsast, mis mõjutas nii metsas kui niidul kasvavate liikide arvu katsealade prooviruutudel.

Vajadus edasiseks uurimiseks

Doktoritöö raames tehtud uuringud kavandati pikaajalise uurimisprogrammi osana. Tulevikus on plaanis korduskirjeldused, mille eesmärgiks on välja selgitada, kas lühikese raieringiga majandatavate istandike alustaimestik jääb pikas perspektiivis kohalike lehtpuumetsade alustaimestikust erinevaks. Samuti peavad korduskirjeldused võimaldama hinnata metsamajanduslike tegevuste mõju lehtpuuistandike alustaimestikule. Lisaks soontaimedele ja sammaldele on oluline ka teiste elustikurühmade monitooring.

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I

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Floristic diversity responses in young hybrid aspen plantations to land-use history and site preparation treatments

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ABSTRACT

Floristic diversity was studied in 7- to 8-year-old commercial hybrid aspen (*Populus tremula* L. × *Populus tremuloides* Michx.) plantations on abandoned agricultural sites with a different land use (grassland or crop field) and site preparation (whole-area ploughing or strip tillage) history. The aim of the study was to investigate how the understorey vegetation had developed in such repeatedly disturbed communities and which environmental variables had significantly affected this. A total of 204 vegetation plots (2 m × 2 m) were established within 51 experimental areas; vegetation descriptions were compiled, concentrations of total N, extractable P and K, and pH of the soil humus layer were determined, and canopy cover of the trees was estimated. Weighted average Ellenberg values for light, moisture, pH, and nitrogen, as well as several life-history characteristics, were calculated for the vegetation plots. Altogether 191 vascular plant species were described: on average 16.7 ± 0.4 species per plot and 28.6 ± 1.1 species per experimental area. Former land use and site preparation method had a significant impact on the position of vegetation plots in detrended correspondence analysis (DCA) ordination, confirmed also by the multiresponse permutation procedure (MRPP). Soil characteristics were significantly correlated with DCA axes. Former land use and site preparation method also affected the species composition. All sites were dominated by competitor species; ruderals were represented in a higher proportion in former fields and whole-area ploughed sites. Species richness and Simpson's diversity index were higher in plantations where strip tillage had been used for site preparation and lower on sites with higher nutrients concentrations in the humus layer. Generally, overstorey vegetation, characterized in the current study using canopy cover, had not started to affect understorey vegetation in young plantations. Application of less intensive site preparation methods is recommended in order to support higher species richness and lower share of ruderal species.

1. Introduction

As a result of the rising demand for timber, pulpwood, bioenergy and several other products from woody plants, the area under forest plantations is continuously increasing in the world (Evans, 2004; FAO, 2005). Further advantages of plantations include the reduction of timber harvested from natural forests and the accumulation of atmospheric carbon in order to slow down global warming. Meanwhile, more attention is paid to the biodiversity of forest plantations, including floral diversity (Moore and Allen, 1999; Hartley, 2002).

Hybrid aspen (*Populus tremula* L. × *Populus tremuloides* Michx.) has received attention in the Baltic Sea region due to its fast growth, cold-hardiness and suitability for the production of pulpwood and bioenergy. It has been recommended as an alternative species for the afforestation of abandoned agricultural lands (Liesebach et al., 1999; Karacic et al., 2003). Recent studies have mainly focused on biomass production, clonal tests, and site-growth relations of hybrid aspen (Yu and Pulkkinen, 2003; Karacic et al., 2003; Rytter and Stener, 2003; Rytter, 2006; Tullus et al., 2007). Studies of floristic diversity have been rare in commercial hybrid aspen plantations in the Baltic Sea region. The floristic diversity of hybrid aspen plantations has been briefly analysed together with other fast-growing poplar plantations on former arable land in Germany (Heilmann et al., 1995) and Sweden (Weih et al., 2003) and in exhausted oil shale quarries in Estonia (Tullus et al., 2008).

Typical secondary successional processes cause changes in the understorey vegetation of forest plantations with additional influences coming from the tree canopy and root-related factors

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(Brockerhoff et al., 2003; Newmaster et al., 2006). Thus, plantation age is associated with plant species composition, richness, and diversity. Young plantations have shown higher species diversity and richness compared to older plantations. This is due primarily to colonization by light-demanding ruderal species, which are suppressed as soon as light availability in the ground layer decreases (Nagaike et al., 2003). Forest species tend to increase in abundance during succession, depending on distance from colonization sources (Dzwonko, 2001; Verheyen et al., 2003). In the current study, we investigated whether the overstorey impact on the understorey vegetation characteristics is significant in young sparsely spaced hybrid aspen plantations on abandoned agricultural land.

Silvicultural treatments used for plantation management also play a significant role in vegetation development (Lindgren and Sullivan, 2001; Nagaike, 2002; Ito et al., 2006; Nagai and Yoshida, 2006), and may even set a plant community back to an earlier successional stage. Site preparation is common practice in the establishment of plantations. Depending on the nature and intensity of the site preparation method, some or the majority of the existing vegetation could be removed, consequently affecting the species richness and diversity of the plant cover (Haeussler et al., 2002; Newmaster et al., 2007). We compared the understorey responses to two site preparation methods with different intensities (strip tillage and whole-area ploughing) in young plantations.

Land use history is another important factor affecting the vegetation of forest plantations (e.g. Ito et al., 2004; Wulf, 2004; Gachet et al., 2007). Former land use impacts soil structure and chemistry, consequently influencing the succession of the understorey, and this effect may remain visible for long periods of time, varying from decades to centuries (Honnay et al., 1999; Graae et al., 2003; De Keersmaker et al., 2004; Falkengren-Grerup et al., 2006). The significant relations between physicochemical soil properties (e.g. moisture conditions, pH, concentrations of the major mineral nutrients) and vegetation traits in plantations have been described in several studies (Ferris et al., 2000; Lu et al., 2006; Prach and Řehounková, 2006). We included the physicochemical soil properties and former land use (crop field or grassland) as potential site factors when explaining the variation in the understorey vegetation characteristics.

The aim of the current study was to investigate how understorey vegetation characteristics in young commercial hybrid aspen plantations are related to previous agricultural land use, site preparation method used for the establishment of these plantations, physicochemical soil properties and overstorey canopy cover. The following hypotheses were formulated:

(i) a less intensive mechanical site preparation method (strip tillage) will support higher vascular plant species richness (S) and diversity (D') compared to full-area ploughing;
(ii) differences in the concentrations of the major mineral nutrients, the acidity of the humus horizon and the moisture condition of the previous field soils will affect vegetation patterns;
(iii) former agricultural land use (crop field or grassland) and site preparation method will affect the species composition;
(iv) the overstorey will influence the understorey vegetation characteristics.

2. Materials and methods

2.1. Study area

The study uses 7- to 8-year-old commercial hybrid aspen plantations established in 1999 and 2000 on former agricultural land mostly in the southeastern and central part of continental Estonia (Fig. 1, Table 1). The land had previously been used as crop fields (number of experimental plots $n = 28$) or grassland ($n = 23$). Before planting 1-year-old micro-propagated hybrid aspens belonging to 27 clones (Tullus et al., 2007), site preparation was carried out. The plantation areas were either ploughed completely ($n = 18$, referred

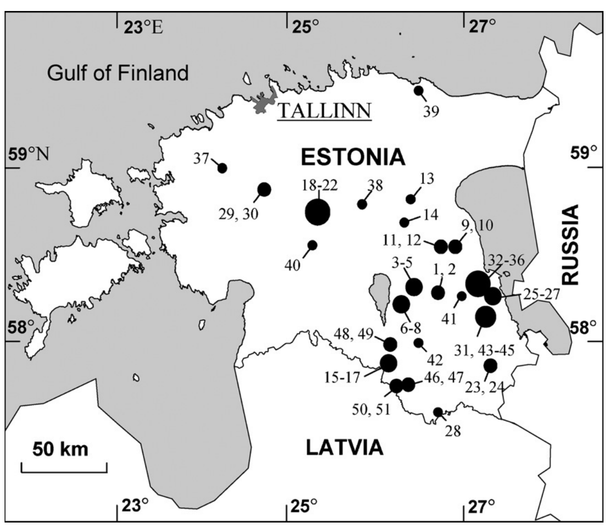

Fig. 1. Locations of the studied hybrid aspen plantations (marked with black dots) and experimental areas (size of the dots is related to the number of experimental areas within the plantations). Numbers of the experimental areas are explained in Table 1.

Table 1
General characteristics of the experimental areas, for the locations on the map please see Fig. 1.

No.	Noltfox ID/exp. no.[a]	Geographic coordinates	Previous land use	Site preparation	Soil moisture condition	Canopy cover of trees (%)
1	101/HHB1	58°16′N; 26°39′E	F[b]	ST[c]	1[d]	19
2	101/HHB2	58°16′N; 26°39′E	F	ST	2	7
3	102/HHB3	58°19′N; 26°33′E	F	WAP	1	63
4	102/HHB4	58°19′N; 26°33′E	F	WAP	1	16
5	102/HHB5	58°19′N; 26°33′E	F	WAP	1	59
6	103/HHB6	58°11′N; 26°18′E	F	WAP	1	33
7	103/HHB7	58°11′N; 26°18′E	G	WAP	2	33
8	103/HHB8	58°11′N; 26°18′E	G	WAP	3	31
9	104/HHB9	58°29′N; 26°54′E	G	WAP	H	35
10	104/HHB10	58°30′N; 26°54′E	G	WAP	1	59
11	105/HHB11	58°30′N; 26°50′E	F	WAP	3	28
12	105/HHB12	58°30′N; 26°50′E	F	WAP	2	18
13	106/HHB13	58°49′N; 26°22′E	G	ST	3	12
14	107/HHB14	58°41′N; 26°19′E	G	WAP	3	41
15	108/HHB15	57°52′N; 26°06′E	G	ST	2	17
16	108/HHB16	57°52′N; 26°06′E	G	ST	2	20
17	108/HHB17	57°52′N; 26°06′E	F	ST	1	29
18	109/HHB18	58°43′N; 25°20′E	F	ST	1	47
19	110/HHB19	58°43′N; 25°20′E	F	ST	2	42
20	110/HHB20	58°43′N; 25°19′E	F	ST	2	13
21	110/HHB21	58°43′N; 25°19′E	F	ST	2	18
22	110/HHB22	58°43′N; 25°20′E	G	ST	1	11
23	111/HHB23	57°52′N; 27°14′E	F	WAP	1	26
24	111/HHB24	57°52′N; 27°14′E	F	WAP	1	11
25	112/HHB25	58°10′N; 27°24′E	G	ST	1	32
26	112/HHB26	58°10′N; 27°24′E	G	ST	2	63
27	112/HHB27	58°10′N; 27°24′E	G	ST	2	30
28	113/HHB28	57°33′N; 26°39′E	G	ST	3	15
29	114/HHB29	58°53′N; 24°41′E	F	WAP	1	31
30	114/HHB30	58°53′N; 24°41′E	F	WAP	1	9
31	115/HHB31	58°07′N; 27°12′E	F	WAP	1	27
32	116/HHB32	58°13′N; 27°18′E	G	ST	1	24
33	116/HHB33	58°13′N; 27°18′E	G	ST	1	7
34	116/HHB34	58°13′N; 27°18′E	G	ST	1	20
35	116/HHB35	58°13′N; 27°19′E	G	ST	3	16
36	116/HHB36	58°13′N; 27°18′E	F	ST	2	5
37	117/HHB37	59°00′N; 24°16′E	G	ST	3	5
38	118/HHB38	58°47′N; 25°51′E	G	ST	1	4
39	119/HHB39	59°29′N; 26°34′E	G	ST	1	6
40	120/HHB40	58°35′N; 25°14′E	G	ST	2	59
41	121/HHB41	58°13′N; 26°57′E	F	ST	1	24
42	122/HHB42	57°58′N; 26°29′E	G	ST	2	38
43	123/HHB43	58°07′N; 27°12′E	F	ST	2	42
44	123/HHB44	58°07′N; 27°12′E	F	ST	3	17
45	123/HHB45	58°07′N; 27°12′E	F	ST	1	21
46	124/HHB46	57°46′N; 26°16′E	F	ST	1	3
47	124/HHB47	57°46′N; 26°15′E	F	ST	1	45
48	125/HHB48	57°54′N; 26°06′E	F	WAP	2	72
49	125/HHB49	57°54′N; 26°06′E	F	WAP	1	25
50	126/HHB50	57°45′N; 26°15′E	G	ST	2	30
51	126/HHB51	57°45′N; 25°15′E	F	ST	1	1

[a] Experimental area identification number according to Noltfox online database (http://noltfox.metla.fi);
[b] F: crop field, G: grassland.
[c] ST: strip tillage, WAP: whole-area ploughing.
[d] Soil moisture regime: 1: automorphic, 2: semi-hydromorphic, 3: hydromorphic, H: histosol.

as whole-area ploughing in the current study), or only furrows marking the tree lines were ploughed ($n = 33$, referred as strip tillage). No chemical vegetation treatment was applied; however, in areas with exceptionally intensive grass growth, the grass was flattened around the trees by foot one or two times during the first season after planting. The former field soils in the study area were mainly auto-, semihydro- or hydromorphic soils with sandy loam and loamy sand dominant profile texture. The soils have been described in detail in a previous study (Tullus et al., 2007).

The average spacing of hybrid aspen plantations was quite even, varying between 1200 and 1600 trees ha^{-1}. In order to study relations between the ground vegetation layer and trees, percentage canopy cover was used, indicating both the light conditions in the ground layer and the growth speed of trees. In the studied young monocultural and evenly structured plantations the overstorey canopy cover was significantly related to the plantation basal area ($R = 0.92$; $p < 0.001$) and the mean height of the trees ($R = 0.91$; $p < 0.001$), confirming the reliability of using canopy cover as a surrogate for plantation productivity. Canopy cover can also be seen as an indirect measure of the root competition intensity with the trees. Due to sparse spacing and considerably variable growth of the trees, it was decided to use canopy cover both as a continuous and categorical effect. The plantations were divided into two groups, with canopy cover above and below 45%, respectively.

2.2. Experimental plots

In the studied hybrid aspen plantations, a long-term network of 51 experimental circle plots (each 0.1 ha) had been previously created for the study and monitoring of growth traits and biomass production of hybrid aspens and tree–soil interactions (Tullus et al., 2007). The centre of each circle plot is marked and, in addition, GPS coordinates have been recorded (Table 1). As part of the current study, four vegetation plots (each 2 m × 2 m) were established within each circle plot and the canopy diameter of all the trees within the circle plots was measured and percentage canopy cover computed. In every vegetation plot a list of vascular plant and moss species was compiled. The total percentage cover of the field and moss layers and the percentage cover of individual species were recorded. The nomenclature follows the atlases of Estonian vascular plants (Kukk and Kull, 2005) and bryophytes (Ingerpuu and Vellak, 1998).

2.3. Soil analysis

In the centre of each vegetation plot, four subsamples were taken from the middle part of the soil humus layer and mixed to form a 0.5-kg composite sample in which pH_{KCl} and concentrations of total nitrogen (N) and extractable phosphorus (P) and potassium (K) were determined. Analyses were performed by the Laboratory of Agrochemistry of the Agricultural Research Centre in Saku [http://pmk.agri.ee], using methods: pH: ISO 10390; total N: ISO 11261; P, K: Mehlich III. The experimental areas were grouped according to soil moisture conditions (Table 1) based on an earlier study (Tullus et al., 2007).

2.4. Data analysis

Several floristic traits were used to characterize the vascular plants growing in the ground vegetation layer of hybrid aspen plantations. Ellenberg values for light, moisture, pH and nitrogen were assigned to vascular plant species according to Lindacher (1995) and weighted average Ellenberg values were calculated for each plot. Based on the BIOFLOR database (Klotz et al., 2002) covering the biological and ecological traits of the flora of Germany, which includes all the vascular plant species from our study, species were classified by habitat preference into the following categories: forest species, grassland species, forest and grassland species, fallow species, grassland and fallow species. Ecological strategy types (competitors, competitors/ruderals, competitors/stress-tolerators, competitors/stress-tolerators/ruderals and ruderals) were assigned to the studied species according to Grime (2001). Life-span categories (annuals, biennials and perennials) were assigned according to Leht (1999).

The general characteristics were calculated using the data matrix of 204 vegetation plots × 191 vascular plant species. Experimental area 121/HHB41 (four plots) was excluded from further analysis due to the radically different vegetation structure and composition—the area was dominated by *Galega orientalis*, which had been grown there for fodder during the previous land use and which is known as an invasive alien species in Estonia (Kull, 2005). Experimental area 104/HHB9 was excluded from the plant–soil analysis due to the extreme soil conditions (Histosol). Descriptive statistics and Spearman rank correlations between the floristic and environmental variables were calculated with Statistica 7 (StatSoft, Inc., 2004).

Species richness (S) and Simpson's diversity index (D') were estimated for all plots with PCORD-4 (McCune and Mefford, 1999) as follows:

$$\text{Species richness} = n \tag{1}$$

$$\text{Simpson's}\, D' = 1 - \sum (p_i^2) \tag{2}$$

where n is the number of species present in the vegetation sample plot and p_i is the proportion of the sample belonging to the ith species.

The studied variables contained both experimental area and vegetation plot level data. Therefore, a two-level hierarchical model was built in order to evaluate the effect of environmental variables on the vegetation plot level species richness and diversity using PROC MIXED with SAS for Windows 9.1.3 (SAS Institute 2002/2004; Littell et al., 2002) and MLwiN (Goldstein et al., 1998). The normality of S and D' was checked with Kolmogorov–Smirnov and Shapiro–Wilk's tests. The distribution of S did not differ from normal distribution at $p < 0.05$ according to both tests; D' was square-transformed, after which its normality was confirmed using the Kolmogorov–Smirnov test. The concentrations of N, P and K and pH of the soil humus layer were treated as plot-level fixed effects, and soil moisture condition (M), plantation canopy cover (C), previous land use (PLU) and site preparation method (SP) as experimental area level fixed effects. PLU and SP were used as dummy variables. Effect of experimental area was treated as a random variable with normal distribution. As a result, the following model was constructed:

$$Y_{ij} = \beta_0 + \beta_1 \cdot \mathrm{SP}_j + \beta_2 \cdot \mathrm{PLU}_j + \beta_3 \cdot M_j + \beta_4 \cdot C_j + \beta_5 \cdot \mathrm{pH}_{ij} + \beta_6 \cdot \log N_{ij} + \beta_7 \cdot \log P_{ij} + \beta_8 \cdot \log K_{ij} + u_{0j} + e_{0ij} \tag{3}$$

where Y_{ij} is the plot level species richness or diversity index, β_0 is the intercept, $\beta_1 \ldots \beta_8$ are the coefficients for the fixed effects at experimental area (j) and plot (ij) level, u_{0j} is the random error at experimental area level: $u_{0j} \sim N(0,\mathrm{var}(u))$, and e_{0ij} is the random error at plot level: $e_{0ij} \sim N(0;\mathrm{var}(e))$.

In order to analyse the positioning of vegetation plots along the ordination axes, Detrended Correspondence Analysis (DCA, Hill, 1979) was applied with default options. To interpret the ordination axes, Spearman rank correlations between plot scores and soil variables were calculated. The Kruskall–Wallis test was used to test the significance between group means of DCA axis1 and axis2 scores followed by the Mann–Whitney U-test.

Differences in vascular plant community composition between groups formed on the basis of land use history, site preparation method and canopy cover were also tested with Multiresponse Permutation Procedures (MRPP) using the Euclidean distance measure. Both DCA and MRPP were performed with PCORD-4; species with less than two occurrences were excluded.

The significance of differences in the frequency of occurrence of common vascular plant species between former crop fields vs. grasslands and ploughed vs. furrowed sites was tested using SAS's PROC GENMOD, followed by ESTIMATE statement (chi-square test). The species that were present in at least 10% of all studied vegetation plots (i.e. on >20 plots out of 200) were included.

We applied only statistical methods that did not assume equality of the groups since we had to make some compromises in the experimental design of the study area and relied on earlier site selection as explained in the description of the study area and experimental plots. The mean values are followed by ±standard error in the text. Level of significance α = 0.05 was applied in all cases.

3. Results

3.1. General characterization

Altogether 191 vascular plant species were found in 204 sample plots; the mean number of species was 16.7 ± 0.4 per plot, varying between 4 and 30 (Fig. 2). The mean number of species in an experimental area (based on four vegetation plots) was 28.6 ± 1.1 species, varying between 8 and 42. Among all vascular plant species, 59% were typical grassland species, 23% fallow species, 8% forest species, 6% grassland and fallow species, 4% forest and grassland species. As shown in Fig. 3, the majority of the species were half-light species (most frequent Ellenberg value for light was 7), preferring

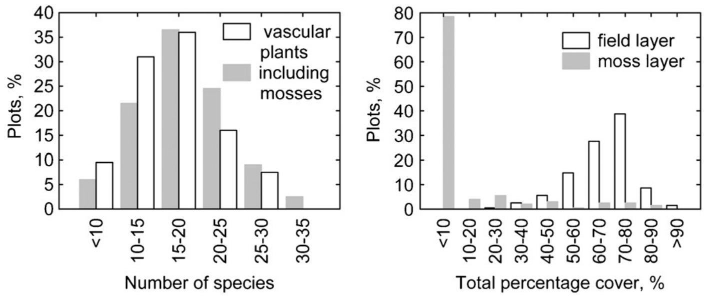

Fig. 2. Distribution of the vegetation plots by number of species and total percentage cover of the field and moss layers.

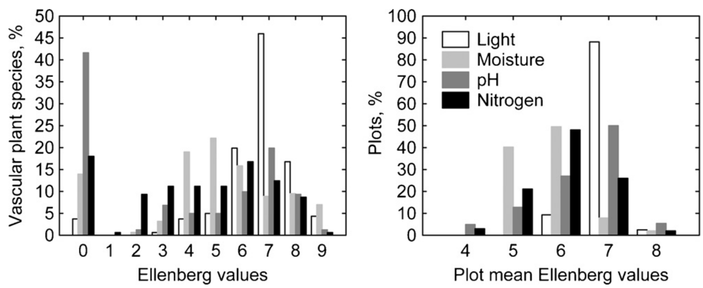

Fig. 3. Distribution of vascular plant species' and plot mean Ellenberg values.

sites with average moisture conditions (most frequent Ellenberg value for moisture was 5). Ellenberg values (except the value for light) showed weak but significant correlations with corresponding environmental variables (Table 2).

The total percentage cover of the field layer varied between 30 and 92%, with an average value of $70.1 \pm 0.8\%$ (Fig. 2). It was in significant, although weak correlation with the plantation canopy cover, both when the canopy cover was treated as a continuous variable (Spearman $R = -0.23$, $p > 0.001$) or as a grouping variable ($F_{1,194} = 3.8184$, $p = 0.05$). The mean percentage cover of the field layer in more shaded plantations (canopy cover >45%) was $67.2 \pm 1.5\%$ compared to $71.0 \pm 1.0\%$ in less shaded ones.

Forty-four bryophyte species were found in the vegetation plots. Moss layer was totally absent in 17 plots and one experimental area. The percentage cover of the moss layer was below 10% in most (79%) of the plots (Fig. 2). In plots with existing moss layer, the mean number of moss species was 2.0 ± 0.1, varying between 1 and 6. The most frequent species (present in >10% of plots) were: *Eurhynchium hians* (35.3% of plots), *Eurhynchium praelongum* (17.2%), *Brachythecium rutabulum* (17.2%), *B. salebrosum* (16.2%), *Brachythecium albicans* (12.3%) and *Plagiomnium cuspidatum* (11.8%). Since the percentage cover and species number of the moss layer were small, it was decided to exclude mosses from further analyses in the current study.

Table 2
Spearman rank order correlations between vegetation plot mean Ellenberg values and corresponding environmental variables.

Ellenberg value	Environmental variable	Spearman *R*	*p*
N	Humus horizon total *N*	0.24	0.001
Light	Canopy cover	0.06	0.406
Moisture	Soil moisture condition	0.21	0.003
pH	Humus horizon pH	0.24	0.001

3.2. Species richness and Simpson's diversity index

According to the model (Table 3), species richness and Simpson's diversity index were influenced by site preparation method. Fewer species appeared in the areas where whole-area ploughing had been applied. 17.9 ± 0.5 species on average were found in strip-tilled sites and 15.3 ± 0.5 species in whole-area ploughed sites; the difference was also confirmed by ANOVA ($F_{1,198} = 11.853$, $p < 0.001$). Higher concentrations of major mineral nutrients in the humus horizon significantly reduced the species richness.

3.3. Vegetation patterns and environmental factors

3.3.1. DCA ordination and MRPP analysis

The position of the vegetation plots in the ordination plot of the first two DCA axes was related to the previous land use and site preparation method and did not differ between the plantations with high (>45%) and low canopy cover (Fig. 4). The ordination axes were correlated with soil moisture, pH_{KCl}, and concentrations of NPK in the humus horizon. The interpretation of DCA was confirmed by MRPP analysis (Table 4).

3.3.2. Species composition

We investigated the frequency of occurrence of 47 typical vascular plant species that were present in at least 10% of all studied vegetation plots (i.e. on >20 plots out of 200) in different site groups according to previous land use and site preparation method (Table 5).

Table 3
Solution for the two-level hierarchical model (SAS's PROC MIXED) describing the effect of environmental variables on vascular plant species richness and Simpson's diversity index, similar results were obtained with MLwiN (data not shown).

Variable	Species richness		Simpson's diversity index	
	F-value	*Pr > F*	*F*-value	*Pr > F*
Type 3 tests of fixed effects				
Site preparation	4.33	0.039	5.12	0.025
Previous land use	0.26	0.613	0.24	0.625
Soil moisture regime	0.57	0.452	0.28	0.600
Canopy cover	0.09	0.770	0.33	0.565
pH_{KCl}	0.82	0.368	0.74	0.391
Log N	6.36	0.013	5.18	0.024
Log P	4.79	0.030	0.09	0.763
Log K	6.65	0.011	1.14	0.288

Variable	Species richness			Simpson's diversity index		
	Estimate	*t* Value	*Pr* > |*t*|	Estimate	*t*-Value	*Pr* > |*t*|
Solution for fixed effects						
Intercept	34.763	6.58	<0.0001	0.875	3.89	<0.0001
Site preparation effect						
Whole-area ploughing	−2.736	−2.08	0.039	−0.117	−2.26	0.025
Strip tillage	0	–	–	0	–	–
Previous land use effect						
Crop field	−0.646	−0.51	0.613	−0.025	−0.49	0.625
Grassland	0	–	–	0	–	–
Canopy cover	−0.001	−0.29	0.770	−0.001	−0.58	0.565
Humus horizon properties						
Soil moisture regime	−0.685	−0.75	0.452	0.019	0.53	0.600
pH_{KCl}	0.549	0.90	0.368	0.022	0.86	0.391
Log N	−48.965	−2.52	0.013	−1.847	−2.28	0.024
Log P	−3.754	−2.19	0.030	−0.022	−0.30	0.763
Log K	−4.420	−2.58	0.011	−0.082	−1.07	0.288
Covariance parameters	Estimate	*Z*-value	*Pr Z*	Estimate	*Z*-value	*Pr Z*
Experimental area, var(u)	13.275	4.14	<0.0001	0.018	3.83	<0.0001
Vegetation plot, var(e)	7.657	8.46	<0.0001	0.019	8.51	<0.0001
Observations	196			196		

Life expectancy and Grime strategies were used for species characterization (Fig. 5). On the whole, 85% of these species were perennials (including one tree species) and 15% were annuals or biennials. According to Grime strategies, 47% were competitors, 23% were competitors/stress-tolerators/ruderals, 13% were competitors/stress-tolerators, 11% were competitors/ruderals and 6% were ruderals.

The share of annual or biennial plants was higher among the species occurring more frequently in previous crop fields and whole-area ploughed sites. A similar trend occurred for ruderals. In

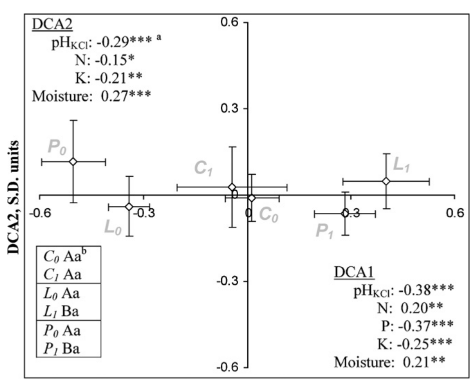

Fig. 4. Group centroids of DCA axis1 (Eigenvalue = 0.63) and axis2 (Eigenvalue = 0.48) scores, whiskers denote standard error of estimate. Group codes: canopy cover of trees: C_0: small, C_1: big; previous land use: L_0: crop field, L_1: grassland; site preparation: P_0: whole area ploughing, P_1: strip tillage. [a]Spearman rank correlations between DCA axis scores and environmental variables, $0.01 < p < 0.05^{*}$; $0.001 < p < 0.01^{**}$; $p < 0.001^{***}$. [b]Capital letters denote significant differences between group mean DCA1 scores and small letters between group mean DCA2 scores as a result of Kruskall–Wallis ANOVA followed by Mann–Whitney *U*-test.

Table 4
Results from MRPP analysis (*T*: test statistic; *A*: chance-corrected within-group agreement).

Factor	*T*	*A*	*p*
Site preparation method	−16.56	0.02	<0.001
Previous land use	−9.97	0.01	<0.001
Plantation canopy cover	−1.63	0.002	0.07

the case of former grasslands and strip-tilled sites, the typical species were perennials with the exception of *Anthriscus sylvestris*. The majority of these species were competitors with no ruderals included.

4. Discussion

4.1. Species richness and diversity

The most important contributors to vascular plant species richness and Simpson's diversity index of the understorey vegetation in young hybrid aspen plantations were site preparation method and concentrations of major mineral nutrients in the humus horizon (Table 3). Species richness was significantly higher in plantations where strip-tillage had been practiced. Obviously, vascular plant cover that had developed after intensive agricultural land-use was left quite undisturbed in the 3–4-m gaps between the furrows, whereas the ploughed strips allowed the colonization of new species. The relation between the intensity of site preparation and its impact on vegetation development has been observed also in other studies (Haeussler et al., 2002; Newmaster et al., 2007). Species richness and diversity were significantly reduced by higher nutrient concentrations in the humus horizon (Table 3). This is in accordance with several fertilization experiments showing that species richness decreases with nutrient addition (e.g. Wilson and Tilman, 2002; Hejcman et al., 2007).

4.2. Species composition and environmental factors

The vascular plant cover of young hybrid aspen plantations was dominated by grassland species and the share of forest plants was small. In general, the scanty occurrence of forest species in the vegetation of fast-growing poplar plantations has been observed both at a young age in Sweden (Weih et al., 2003) as well as in older sparsely spaced plantations in North-East Germany (Zerbe, 2003). The development of vegetation cover is still in a preliminary phase and the observable trends are mostly driven by the disturbances that took place before the establishment of the plantations, including previous agricultural land use and site preparation. An analysis of the occurrence of common vascular plant species (Table 5) suggested that the species composition was related to previous land use and site preparation method. However, it should be pointed out that 78% of the former grassland sites were prepared by strip tillage. This helps to explain why some species occurring mostly in former grasslands were more frequently found in strip-tilled areas. In the case of former fields, both site preparation methods had been applied almost equally. Typical field species (e.g. *Matricaria perforata* and *Myosotis arvensis*) occurred more often in the vegetation cover of plantations established in former fields where whole-area ploughing had been applied for site preparation. Typical grassland species (e.g. *Dactylis glomerata*, *Deschampsia cespitosa* and *Lathyrus pratensis*) dominated in former grasslands and strip-tilled areas (Table 5). All sites were dominated by competitors—common species in productive habitats (Fig. 5). Ruderal species were represented in a higher proportion in former fields and whole-area ploughed sites. These areas can be described as fertile sites, repeatedly disturbed by cultivation activities. In such conditions, the persistence of ruderals was probably supported by their high seed production and the ability of the seeds to remain dormant in the soil for long periods of time (Grime, 2001).

The detrended correspondence analysis (Fig. 4) confirmed the significant impact of previous land use and site preparation method on vascular plant cover in young plantations on abandoned agricultural land. At the same time, it indicated the heterogeneity of the vegetation since the significant differences in group centroids appeared only in the first ordination axes and they were concentrated in a rather small area comprising ±0.5 standard deviation units of the whole variation. Former fields and whole-area ploughed sites stood closer to each other in the negative side of DCA1, as did former grasslands and strip-tilled sites in the positive side. This position could be partly explained by the more frequently used site preparation method for former grasslands, as discussed earlier. Both DCA axes were positively correlated with soil moisture value. In general, moist sites are more often used as grasslands rather than crop fields and grassland sites also appeared in the positive side of DCA1.

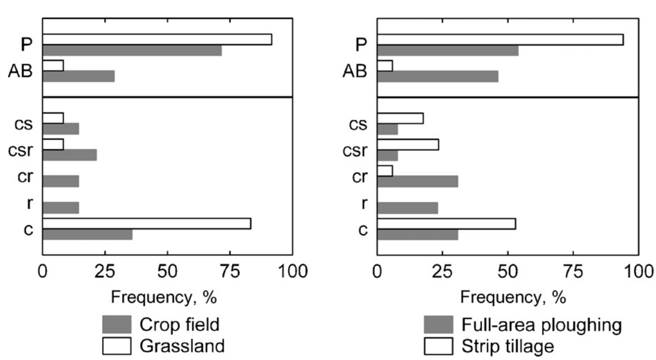

Fig. 5. Life expectancy (AB: annuals and biennials, P: perennials) and Grime strategies (cs: competitors/stress-tolerators, csr: competitors/stress-tolerators/ruderals, cr: competitors/ruderals, r: ruderals, c: competitors) of vascular plant species appearing significantly more frequently at sites with different former land use and site preparation history.

Table 5
The frequency of occurrence of common vascular plant species at sites with different former land use and site preparation history and the significance of differences according to chi-square test. The species that were present in at least 10% of all studied vegetation plots were included.

Vascular plant species	Former land use			Site preparation method		
	Crop field (%)	Grassland (%)	*p*	Whole-area ploughing (%)	Strip tillage (%)	*p*
Achillea millefolium	51	59	0.272	46	59	0.066
Agrostis capillaris	36	36	0.972	21	45	0.001
Agrostis gigantea	38	28	0.149	43	28	0.033
Alchemilla vulgaris (coll.)	11	18	0.144	8	18	0.070
Alopecurus pratensis	3	33	<0.001	13	19	0.256
Anthriscus sylvestris	25	52	<0.001	7	55	<0.001
Artemisia vulgaris	69	34	<0.001	74	41	<0.001
Betula pendula	19	3	0.002	25	5	<0.001
Campanula patula	16	5	0.026	10	12	0.665
Cerastium fontanum	50	35	0.031	60	34	<0.001
Cirsium arvense	81	79	0.704	88	77	0.065
Dactylis glomerata	30	50	0.004	10	55	<0.001
Deschampsia cespitosa	5	28	<0.001	6	21	0.007
Elymus repens	82	75	0.202	88	74	0.030
Epilobium montanum	21	1	0.002	17	9	0.132
Epilobium parviflorum	25	1	0.001	33	3	<0.001
Equisetum arvense	49	48	0.860	38	55	0.020
Fallopia convolvulus	18	10	0.117	22	9	0.014
Festuca pratensis	11	16	0.287	4	19	0.008
Festuca rubra	27	39	0.066	10	45	<0.001
Galium album	23	40	0.010	7	45	<0.001
Gnaphalium uliginosum	34	7	<0.001	33	15	0.003
Hypericum maculatum	15	10	0.287	10	14	0.376
Hypericum perforatum	22	14	0.145	22	16	0.311
Lathyrus pratensis	19	47	<0.001	6	47	<0.001
Leucanthemum vulgare	36	20	0.011	22	32	0.142
Lysimachia vulgaris	11	10	0.760	7	13	0.225
Matricaria perforata	20	7	0.007	22	9	0.014
Mentha arvensis	19	30	0.050	22	25	0.659
Myosotis arvensis	33	14	0.002	50	10	<0.001
Phalaris arundinacea	0	23	0.001	11	10	0.833
Phleum pratense	79	64	0.023	61	78	0.011
Plantago major	12	11	0.797	19	7	0.011
Poa angustifolia	15	36	0.001	15	30	0.025
Poa palustris	16	13	0.590	7	19	0.029
Poa trivialis	22	7	0.003	13	16	0.459
Potentilla anserina	10	20	0.064	6	20	0.012
Ranunculus repens	16	18	0.608	6	23	0.003
Sonchus arvensis	39	30	0.212	47	28	0.007
Stachys palustris	2	22	<0.001	6	14	0.075
Stellaria graminea	21	17	0.488	6	27	0.001
Taraxacum officinale (coll.)	91	78	0.016	89	83	0.252
Trifolium hybridum	26	11	0.009	24	16	0.215
Tussilago farfara	23	28	0.409	26	25	0.829
Veronica chamaedrys	19	32	0.035	7	34	<0.001
Vicia cracca	37	58	0.004	25	59	<0.001
Vicia hirsuta	31	23	0.221	42	19	<0.001

The strongest relations with DCA1 were found for pH_{KCl} and the concentration of phosphorus; DCA2 was more strongly related to soil moisture. The impact of soil moisture and pH on the vegetation are considered to be among the strongest for ecological factors (Hokkanen, 2006; Lu et al., 2006). In our study, the importance of soil moisture, pH, and concentrations of nutrients for the vegetation of young plantations was also confirmed by significant relations between Ellenberg values and the corresponding soil variables (Table 2).

MRPP analysis showed differences between the studied site groups similar to those found with DCA. Nevertheless, the *A* values were very small (Table 4), also indicating a strong within-group heterogeneity.

4.3. Overstorey influence

The typical vascular plant species in young hybrid aspen plantations can be characterized as light-demanding competitive species, which is in accordance with results from other studies in young forests, e.g. Bossuyt and Hermy (2000). We can predict a gradual decrease in their share during the latter successional stages when the understorey light conditions worsen due to increasing canopy cover of the trees. In the vegetation of abandoned agricultural areas, plant species with lower Ellenberg values for light (3–6) are more likely to persist during the succession (Harmer et al., 2001).

In the current study, no significant relation between canopy cover and Ellenberg value for light was found (Table 2), although there was a weak correlation between canopy cover and percentage cover of the field layer. The latter can be explained by the fact that the plantations are young and quite sparsely spaced, so even in plantations with the highest canopy cover (in our study 45–72%), canopy closure had only just started to occur during the last 1–3 years, and it is obvious that the understorey is likely to respond to changes in light availability with some delay, as also pointed out by Brockerhoff et al. (2003).

4.4. Management implications

4.4.1. Plantation forests on abandoned agricultural land: productivity vs. biodiversity

The studied plantations were established on former agricultural land, representing therefore communities repeatedly disturbed by human activities. Anthropogenic disturbances will also continue in the future in the form of short-rotation forestry practices. On the one hand, economic profitability is considered more important than the issue of biodiversity under these circumstances. On the other hand, thorough knowledge of the ecological processes taking place in these conditions is needed to avoid negative impacts on the environment, particularly if the area under short-rotation forestry continues to grow. Ideally, a landowner establishing a forest plantation should also pay attention to the factors influencing biodiversity, and apply appropriate methods (site preparation, tree species selection, silvicultural practices, rotation length) depending on soil properties, land use history, surrounding communities and landscape.

The results of our study supported the commonly known contradiction between the simultaneous achievement of a fast growth rate of the trees together with high species richness and diversity. More fertile sites favour the productivity of the trees but not the species richness of the ground vegetation layer. Poplars and aspens are known as species that prefer fertile sites, especially in short-rotation plantations (Stanturf et al., 2001). Already at an early age, the growth rate of hybrid aspen showed a positive correlation with the concentration of extractable P in the previous field soils (Tullus et al., 2007). We can predict that a high concentration of nutrients in the soil humus layer of fast-growing deciduous plantations will persist during the whole rotation. Affected initially by the fertilization practices during the previous agricultural land use, it will later be influenced by the nutritious aspen leaf litter and N-fixing mycorrhiza.

Although nutrient-rich soil does not support high species richness of the understorey vegetation, site requirements of fast-growing tree species should be met first when establishing forest plantations. High biodiversity of aspen forests is usually related to old economically over-mature stands. Old aspen forests and aspen trees are associated with a great number of bird, mammal, lichen, moss and vascular plant species, including several red-list species (Harestad and Keisker, 1989; Kuusinen, 1994; Hanski, 1998; Degteva, 2005; Hedenas et al., 2006). Thus, putting the biomass production pressure on short-rotation aspen plantations would help to preserve old aspen forests and the related environmental values. At the same time, forest plantations on former agricultural land have been found to increase the floristic diversity of areas dominated by agriculture, indicating the importance of landscape context for the evaluation of short-rotation forestry plantation effects on biodiversity (Weih et al., 2003).

The possible negative environmental impact of large monocultural stands can also be avoided by setting size limits and/or mixing aspen with other tree species, e.g. shade-tolerant *Picea abies* (L.) H. Karst., which creates more versatile conditions for ground vegetation development.

4.4.2. Site preparation impact on early vegetation and stand development

According to the results of our study, species richness was higher in the sites where strip tillage had been applied (Table 3) and there were no ruderals among the species typical of strip-tilled sites (Fig. 5). Less intensive site preparation treatments tend to favour the existing species, whereas more intensive treatments, which destroy or remove the existing vegetation and vegetative reproductive structures, tend to favour ruderal and invasive species (Haeussler et al., 2002). Ruderal species are able to grow in a large variety of sites including areas degraded by human activities. If the goal of the landowner is to support the compositional quality of the understorey vegetation, the spread of ruderals should not be favoured and less intensive site preparation method should be used for establishing forest plantations.

At the same time, the canopy cover of young hybrid aspen plantations, indicating the survival and growth rate, but also the dimensions of the root system of the trees, was significantly higher ($F_{1,49} = 5.6677$, $p = 0.02$) in plantations where whole-area ploughing had been applied ($34.2 \pm 4.3\%$), compared to strip-tilled plantations ($22.5 \pm 2.8\%$). However, in the long run, strip tillage could also have other advantages, e.g. strip tillage is recommended in order to keep microbiological activity as low as possible and to harmonize N mineralization in the soil and N uptake by trees (Jug et al., 1999).

New descriptions of the study area are planned in order to clarify how the impact of site preparation on the under- and overstorey of hybrid aspen plantations changes in time and to discover when a clearer distinction between plant community types, depending on the effects of stand development and soil conditions, will emerge.

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II

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Change from agriculture to forestry: floristic diversity in young fast-growing deciduous plantations on former agricultural land in Estonia

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The understorey vascular plant cover and its relations with the overstorey tree species and site properties in young silver birch and hybrid aspen plantations were studied. Understorey vegetation was similar in both plantation types in terms of species richness, diversity, sensitivity to human impact, life-span and habitat preference. Nevertheless, in denser silver birch plantations some signs indicated a faster vegetation development overall, e.g., a higher share of shade tolerant plant species. The concentration of total N was higher in the humus layer of silver birch plantations consequently affecting the nutritional status of the understorey vegetation. The significant impact of the plantation type on the understorey vegetation was confirmed by the NMDS analysis. The hypothesis that semi-exotic hybrid aspen plantations may support the spread of alien species or may show a tendency towards smaller indigenous species richness was not confirmed. Irrespective of the overstorey tree species, a strong previous land use impact, i.e. disturbance history, on the ground vegetation was eminent.

Key words: abandoned agricultural land, biodiversity, hybrid aspen, plantation forestry, silver birch, understorey vegetation

Introduction

Forest plantations with fast-growing deciduous trees have been established in hemiboreal Estonia during the last two decades similarly to the other Baltic Sea region countries. At an early age, deciduous trees tend to exceed conifers in biomass productivity in this region (Weih 2004). Traditionally deciduous trees have been disfavoured when managing the conifer dominated forests, however, according to the Centre of Forest Protection and Silviculture (2008), the share of deciduous trees in the growing stock of Estonian forests has risen during the last half-century. On one hand, typical hardwood species (birches, alders and aspens) have become economically more valuable as pulpwood, timber and bioenergy resources since the late 20th century. On the other hand, the share of deciduous tree species has increased as a consequence of natural afforestation of abandonment of agricultural land, since several of them e.g. birches, grey alder and willows are pioneer species at such sites. Agricultural land use has fallen drastically in Estonia during the last decades. Due to political, economical and social changes, one third of the arable land was abandoned at the beginning of the 1990s (Peterson & Aunap 1998). However, natural afforestation is usually a slow and spatially uneven process. Therefore, the establishment of forest plantations with fast growing deciduous trees is recommended as an alternative land use for such areas. At the same time all long-term nature manipulations including management of forests and forest plantations should nowadays be analysed in the light of the predicted climate change. The impact of climatic factors on biodiversity of temperate European ecosystems has been found to be highly significant whereas in the case of vascular plant species richness land use intensity also plays an important role (Dormann *et al*. 2008). Modeling of the impact of climate change on boreal forests has suggested that the biomass productivity of both conifer and deciduous tree species should rise in general (Briceno-Elizondo *et al*. 2006, Garcia-Gonzalo *et al*. 2007). A vegetation shift in a northerly direction is probably going to affect the species composition (Kullman 2008, Morin *et al*. 2008). For hemiboreal forests it means an increasing share of deciduous tree species.

Several hundred hectares of hybrid aspen (*Populus tremula* × *P. tremuloides*) and silver birch (*Betula pendula*) plantations have recently been established in Estonia (Jõgiste *et al*. 2003, Tullus *et al*. 2007). Hybrid aspen has proved to be one of the fastest growing deciduous trees in the Nordic countries, being also sufficiently cold resistant (Yu *et al*. 2001, Weih 2004, Rytter 2006). The recommended rotation period for hybrid aspen is 20–30 years, because up to this age the growth speed of hybrid aspen considerably exceeds its parent species (Heräjärvi & Junkkonen 2006). Silver birch reaches bulk maturity in plantations in 30–40 years.

The increasing area under short-rotation forest plantations also means that their ecological impact is growing. The current study focuses on the vascular plant cover in young hybrid aspen and silver birch plantations on former agricultural land. The understorey vegetation of deciduous plantations on abandoned agricultural land in the boreal vegetation zone is a quite scantily researched topic (Gustafsson 1988, Heilmann *et al*. 1995, Weih *et al*. 2003, Soo *et al*. 2009). Forest plantations on abandoned agricultural land represent associations that have been repeatedly disturbed by human activities during the course of time. Species composition of understorey vegetation is affected by the previous land use (Ito *et al*. 2004, Gachet *et al*. 2007) and the intensity of site preparation and weed control before plantation establishment (Haeussler *et al*. 2004, Miller & Chamberlain 2008). Soil seed bank may influence understorey species composition as well (Zobel *et al*. 2007), although its role in old field forest succession is hardly studied. The anthropogenic impact continues via plantation management activities accompanied by the environmental impact from climate change. During the course of understorey vegetation development in forest plantations, the impact from overstorey trees will gradually rise in the form of intensifying light and root competition, formation of litter layer and consequent changes in physicochemical and biological properties of the humus layer, which in turn may depend on the tree species (Sydes & Grime 1981a, 1981b, Prescott 2002, Janišová *et al*. 2007). The impact of tree species on understorey vegetation is generally acknowledged (Légaré *et al*. 2001, Augusto *et al*. 2003, Qian *et al*. 2003, van Oijen *et al*. 2005). Overstorey composition and structure influence understorey vegetation by changing resource availability (light, water and soil nutrients) and through the physical effects of the litter layer (for detailed literature review *see* Barbier *et al*. 2008). According to some studies deciduous trees support higher understorey diversity than conifers in the boreal zone (e.g. Wallrup *et al*. 2006). There are fewer comparative studies about differences in ground vegetation under different deciduous or different coniferous tree species.

As an important feature of the current study, besides investigating and comparing the understorey vegetation under two economically important deciduous tree species in young plantations we are also comparing vegetation characteristics under silver birch as an indigenous tree species and under hybrid aspen as a semi-exotic species (*P. tremula* is indigenous, *P. tremuloides* originates from North America). Although *P. tremula* and *P. tremuloides* are biologically similar species, some ecological differences have been observed between *P. tremula* and hybrid aspen in Scandinavia and the Nordic countries, which are partly associated with the North-American parent of the hybrid. These differences are related to the phenology and growth speed during the first 15–20 years (Yu *et al*. 2001, Heräjärvi & Junkkonen 2006), different susceptibility to some pests and diseases including those previously not recorded on *P. tremula* but common to *P. tremuloides* (Kasanen *et al*. 2002), differences in the viability of seeds from inter- and intraspecific crosses (Suvanto & Pulkkinen 2004). Thus, from environmental point of view it is important to find out whether hybrid aspen plantations could provide somewhat different site for understorey vegetation as compared with indigenous tree species. In regions, where a great number of various exotic tree species are cultivated, differences between understorey vegetation in indigenous and exotic tree species plantations have also been observed. Sometimes the ground vegetation of exotic plantations incorporates a higher share of exotic plant species (Brockerhoff *et al*. 2003, Mascaro *et al*. 2008, Paritsis & Aizen 2008).

The main research questions of the study were: (i) Are there any significant differences in vascular plant species richness, diversity, composition and ecological characteristics in the ground vegetation layer between young silver birch and hybrid aspen plantations growing on abandoned agricultural land? (ii) Which site and stand related factors have affected the vegetation characteristics? (iii) Does semi-exotic hybrid aspen offers suitable habitat for indigenous vascular plant species, comparable with domestic silver birch?

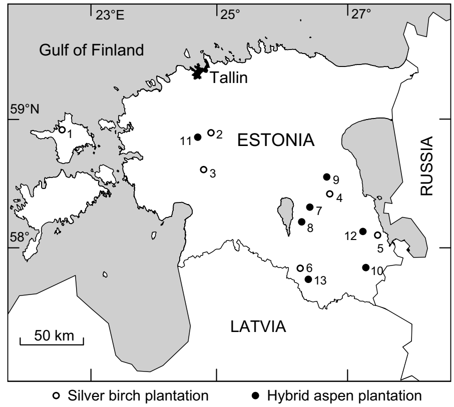

Fig. 1. Locations of the experimental areas. Experimental area numeration is explained in Table 1.

Material and methods

Study area

The study was carried out in 7- to 9-year-old silver birch and hybrid aspen plantations that had been established in 1999 and 2000 on abandoned agricultural land in Estonia. One-year-old silver birch seedlings and micropropagated 1-year-old hybrid aspen plants belonging to 27 different clones had been used as planting material. In order to reduce the heterogeneity of the study area we selected from the network of long-term experimental areas in hybrid aspen and silver birch plantations (Jõgiste *et al*. 2003, Tullus *et al*. 2007) only plantations established on former crop fields, where whole-area ploughing had been used for site preparation. As a result six silver birch and seven hybrid aspen plantations were included in the study (Fig. 1 and Table 1).

Four vegetation plots (each 2 × 2 m) were established within each experimental area. In every vegetation plot a list of vascular plant species was compiled. The total percentage cover of the field layer and percentage cover of individual species were recorded. The nomenclature follows the atlas of the Estonian flora (Kukk & Kull 2005). In order to characterize the impact of trees on the understorey vegetation, diameter of the stem at breast height (DBH) of all the trees within the experimental areas was measured and plantation basal area (BA) per hectare was estimated (Table 1).

Soil analysis

In the centre of each vegetation plot, a soil sample was taken from the middle part of the humus horizon, from which pH_{KCl} and concentrations of total nitrogen (N) and extractable phosphorus (P) and potassium (K) were determined. Analyses were performed by the Laboratory of Agrochemistry of the Agricultural Research Centre in Saku, using methods: ISO 10390 for pH, ISO 11261 for total N, and Mehlich III for P and K. The experimental areas were grouped according to soil moisture conditions (Table 1) according to earlier studies (Jõgiste *et al*. 2003, Tullus *et al*. 2007).

Data analysis

Ellenberg indicator values for light, moisture, pH and nitrogen were assigned to vascular plant species according to Lindacher (1995) and weighted average Ellenberg values were calculated for each plot. Based on the BIOFLOR database (Klotz *et al*. 2002), species were classified by habitat preference into the following categories: forest species, grassland species, fallow species and intermediate types. Life-span categories were assigned to the studied species according to Leht (1999). The status of the species in Estonian flora (native *vs*. alien) was determined based on Kukk and Kull (2005). According to their sensitivity to human impact the studied plant species were divided into the following groups: apophytes, hemeradiaphores and anthropophytes. Apophytes prefer moderate to strong human impact and communities changed by human activities. Hemeradiaphores are indifferent to a certain degree of human activities; such plants are often found in communities with little human influence. Anthropophytes are very rare in natural communities surviving only in communities significantly changed by human activities, e.g arable weeds (Kukk 1999).

Species richness (*S*) and Simpson's diversity index (*D´*) were estimated for all plots with PCORD-4 (McCune & Mefford 1999). In order to investigate how environmental variables (overstorey tree species, stand basal area, soil moisture conditions, N, P, K and pH of the soil humus layer) corresponded to the understorey vegetation, non-metric multidimensional scaling (NMDS) with the community ecology package Vegan 1.15–1 for R (Oksanen *et al*. 2008) was performed. The analysis was run with three data sets: all observations together and both plantation types

Table 1. Main characteristics of the experimental areas (DBH = diameter of the stem at breast height, BA = basal area), for the locations on a map *see* Fig. 1. Letters denote significant differences of means determined by Tukey HSD test ($p < 0.05$) after one-way ANOVA.

No.	Experimental area ID	Geographic coordinates	Tree species	Soil	Density (trees ha^{-1})	DBH (cm)	BA (m^2 ha^{-1})
1	Reigi	58°59´N, 22°32´E	Silver birch	Automorphic	1570	2.0 ± 0.2^{a}	0.7
2	Nadalama	58°54´N, 24°54´E	Silver birch	Automorphic	3070	5.5 ± 0.2^{cd}	7.7
3	Viluvere	58°39´N, 24°51´E	Silver birch	Hydromorphic	2950	4.1 ± 0.1^{b}	4.1
4	Kõrveküla	58°26´N, 26°45´E	Silver birch	Automorphic	1340	3.7 ± 0.2^{b}	1.6
5	Sillapää	58°05´N, 27°26´E	Silver birch	Automorphic	1960	4.5 ± 0.2^{b}	3.5
6	Rampe	57°52´N, 26°12´E	Silver birch	Automorphic	1790	3.6 ± 0.3^{ab}	2.0
7	102/HHB5*	58°19´N, 26°33´E	Hybrid aspen	Automorphic	1280	5.5 ± 0.2^{d}	3.5
8	103/HHB6*	58°11´N, 26°18´E	Hybrid aspen	Automorphic	1180	4.7 ± 0.1^{bc}	2.1
9	105/HHB11*	58°30´N, 26°50´E	Hybrid aspen	Hydromorphic	1130	4.4 ± 0.1^{b}	1.8
10	111/HHB23*	57°52´N, 27°14´E	Hybrid aspen	Automorphic	940	4.1 ± 0.1^{b}	1.4
11	114/HHB30*	58°53´N, 24°41´E	Hybrid aspen	Automorphic	1170	1.7 ± 0.1^{a}	0.4
12	115/HHB31*	58°07´N, 27°12´E	Hybrid aspen	Automorphic	880	4.2 ± 0.2^{b}	1.4
13	125/HHB48*	57°54´N, 26°06´E	Hybrid aspen	Semi-hydromorphic	1190	5.9 ± 0.2^{d}	3.7

* Experimental area identification number according to Noltfox online database (http://noltfox.metla.fi).

separately. In order to explain the ordination, the environmental vectors and a factor (plantation type) were fitted onto the NMDS plots, using the function 'envfit' (Oksanen *et al*. 2008).

The *t*-test was used to test the differences in the group means of experimental area level variables between silver birch and hybrid aspen plantations. The normality of these variables was checked with Shapiro-Wilk's test. In order to compare variables estimated at the vegetation plot level, a MIXED model was applied, with experimental area treated as a random effect using SAS 9.1.3 (SAS Institute Inc., Cary, NC, USA). The significance of differences in the distribution of vascular plant species into ecological groups between hybrid aspen and silver birch plantations was tested using the chi-square test (SAS's PROC GENMOD followed by ESTIMATE statement). In the text, the mean values are followed by ± standard error. Differences are considered significant at $\alpha = 0.05$.

Results

Altogether 84 vascular plant species were found in the studied vegetation plots in hybrid aspen plantations and 83 species in silver birch plantations, the total number of species was 114. The mean species richness on a sample plot was 15.8 ± 0.7 species, varying between 8 and 32 species. In an experimental area (each comprising four plots) 26.9 ± 1.9 species were found on average, varying between 20 and 42 species. Both vegetation sample plot and experimental area level species richness and diversity were similar in silver birch and hybrid aspen plantations (Fig. 2 and Table 2). Neither did the plot mean Ellen-

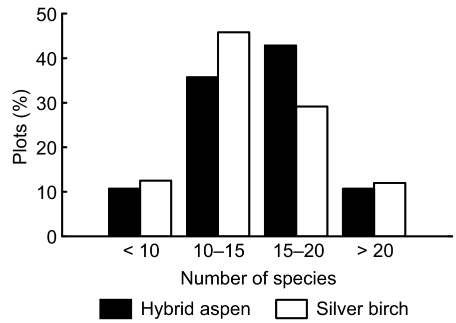

Fig. 2. Distribution of the vegetation plots by number of vascular plant species in silver birch and hybrid aspen plantations.

Table 2. Comparison of ecological characteristics in silver birch and hybrid aspen plantations.

Variable	Hybrid aspen	Silver birch	*t*	Pr > |*t*|
Estimated for each experimental area (*t*-test)				
Trees (ha^{-1})	1110 ± 55	2113 ± 296	–3.60	**0.004**
BA (m^2 ha^{-1})	2.04 ± 0.45	3.25 ± 1.02	–1.14	0.278
DBH (cm)	4.35 ± 0.51	3.90 ± 0.47	0.63	0.544
Total species richness	27.14 ± 2.08	26.67 ± 3.45	0.12	0.905
Estimated for each vegetation plot (MIXED model)				
Soil humus layer properties				
pH	6.01 ± 0.15	6.00 ± 0.18	0.03	0.973
Total N (%)	0.12 ± 0.01	0.18 ± 0.01	–1.99	**0.050**
Extractable P (mg g^{-1})	93.32 ± 9.53	126.79 ± 27.53	–0.63	0.535
Extractable K (mg g^{-1})	122.00 ± 10.01	173.58 ± 18.86	–1.40	0.170
Vegetation traits				
Total cover	64.57 ± 3.02	68.58 ± 3.44	–0.54	0.594
Species richness	15.50 ± 0.72	16.21 ± 1.22	–0.32	0.749
Simpson's diversity index	0.69 ± 0.03	0.76 ± 0.02	–1.01	0.317
Ellenberg values				
Light	7.10 ± 0.06	6.96 ± 0.08	0.97	0.339
Light (3–6), percentage of plants	16.92 ± 1.42	24.74 ± 1.68	–2.55	**0.015**
Light (7–9), percentage of plants	76.18 ± 1.80	68.97 ± 1.80	2.17	**0.036**
Moisture	5.71 ± 0.15	5.73 ± 0.09	–0.06	0.950
pH	6.63 ± 0.21	6.20 ± 0.19	0.83	0.412
Nitrogen	6.08 ± 0.15	6.31 ± 0.13	–0.66	0.513

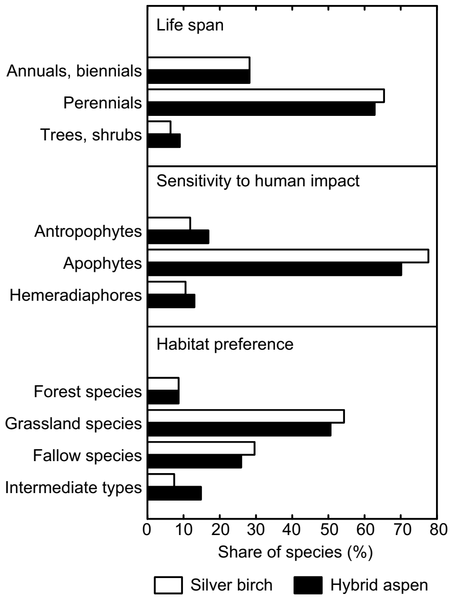

Fig. 3. Distribution of vascular plant species into ecological groups in silver birch and hybrid aspen plantations.

berg values for light, moisture, pH and nitrogen depend on the overstorey species. However, a significantly higher share of shade tolerant species (Ellenberg value 3–6) was found in silver birch plantations and a higher share of half-light and light species (Ellenberg value 7–9) in hybrid aspen plantations (Table 2). The species list of most frequent vascular plant species (present in > 10% of plots), their frequency and mean percentage cover in all plots, and separately in both studied plantation types, is presented in the Appendix.

Among the studied experimental area level characteristics, only plantation density was significantly related to the overstorey tree species, being higher in silver birch plantations. The concentration of total N in the soil humus layer of the vegetation plots was significantly higher in silver birch plantations; other observed soil properties were similar under both species (Table 2).

According to the chi-square test no significant differences were found in the distribution of vascular plant species into habitat preference, sensitivity to human impact, and life span groups between hybrid aspen and silver birch plantations. All experimental areas were dominated by species belonging to similar ecological groups (perennials, grassland species, apophytes) (Fig. 3).

The NMDS ordination did not reveal any considerable groupings of the data. Approximately half of the vegetation plots from both plantation types were situated in the same area in the ordination diagram (Fig. 4A). However, the impact of the overstorey species was statistically significant (Table 3). The soil related variables had significantly affected the positioning of the vegetation plots in the ordination diagram of the whole study area (Fig. 4A) as well as in both plantation types (Fig. 4B and C). As the main difference between the two plantation types, stand basal area was significantly related to the understorey vegetation in silver birch plantations (Fig. 4B) but not in hybrid aspen plantations (Fig. 4C).

Discussion

The understorey vegetation of the studied young silver birch and hybrid aspen plantations was dominated by perennial grassland species irrespective of the overstorey tree species (Fig. 3). This is in accordance with other studies stating that during the transition from agricultural to forest land the ground vegetation will remain different from typical forest vegetation for a long period (Gachet *et al*. 2007). Vascular plant species typical to open-sites will persist. The addition of forest species may be hindered and may be a very long term process governed by dispersal limitations and habitat quality (e.g soil properties) in new forests (Honnay *et al*. 1999, Graae *et al*. 2003, De Keersmaker *et al*. 2004, Flinn & Vellend 2005). The high share of grassland species shows their high inertness and durability in the changing light conditions. However, further studies are needed in order to clarify the share of generative and vegetative individuals among grassland and forest species in relation to plantation density and basal area.

As expected no hemeraphobs (species severely disturbed by human activities) were found from plantations representing communi-

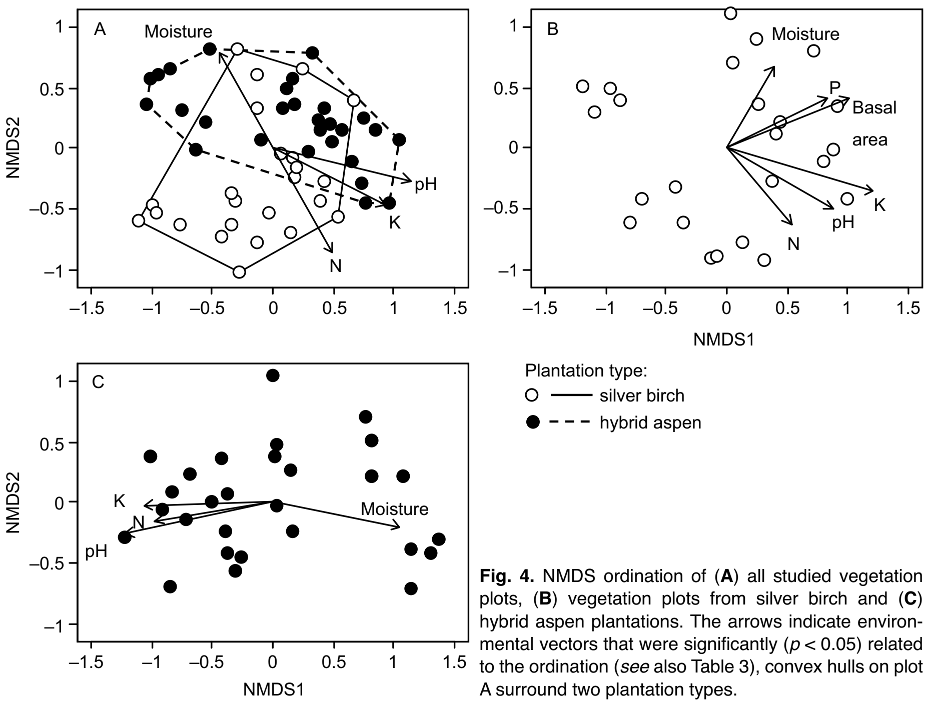

Fig. 4. NMDS ordination of (**A**) all studied vegetation plots, (**B**) vegetation plots from silver birch and (**C**) hybrid aspen plantations. The arrows indicate environmental vectors that were significantly ($p < 0.05$) related to the ordination (*see* also Table 3), convex hulls on plot A surround two plantation types.

ties repeatedly disturbed by human activities (Fig. 3). The studied vegetation was dominated by apophytes which are common to semi-natural communities. The share of hemeradiaphores and anthropophytes was roughly equal. It can be expected that during the following succession, as the impact of previous disturbances decreases, the share of hemeradiaphores is going to rise and the share of anthropophytes will diminish.

As one of the main objectives, the influence of overstorey tree species on the understorey vegetation was studied. Based on the results (Fig. 4, Tables 2 and 3), the overstorey impact has been weaker than that of soil properties. Similar findings have been reported in other studies, showing that the identity of canopy species may be less important than other factors like stand age and site properties (Geldenhuys 1997, Brockerhoff

Table 3. Significance of environmental variables fitted onto NMDS ordination

Environmental variable	Both plantation types		Silver birch plantations		Hybrid aspen plantations	
	r^2	Pr (> *r*)	r^2	Pr (> *r*)	r^2	Pr (> *r*)
Overstorey species	0.14	0.001	–	–	–	–
Basal area	0.05	0.339	0.51	0.001	0.02	0.789
Moisture	0.29	< 0.001	0.26	0.037	0.58	< 0.001
pH	0.48	< 0.001	0.44	0.005	0.78	< 0.001
N	0.35	0.001	0.29	0.038	0.49	< 0.001
P	0.10	0.072	0.37	0.004	0.03	0.672
K	0.38	< 0.001	0.69	< 0.001	0.57	< 0.001

et al. 2003). Légaré *et al.* (2001) showed that species richness, evenness and diversity did not vary significantly with forest overstorey composition, although it had influenced understorey composition. Also in the current study species richness and diversity were similar in both plantation types and a significant but weak relationship between overstorey species and understorey vegetation composition was observed (Fig. 4A and Table 3). It must be pointed out that the studied plantations were rather young and much stronger impact from overstorey tree species can be expected at higher age. The main differences observed in the vegetation characteristics between 7- to 9-year-old silver birch and hybrid aspen plantations could rather be attributed to the differences in stand densities (Table 1), which are associated with different planting densities recommended for establishing hybrid aspen and silver birch plantations in the region. For example the share of shade tolerant vascular plant species (Ellenberg value for light 3–6) was higher under silver birches and the share of half light and light species (Ellenberg value for light 7–9) was higher under hybrid aspens (Table 2). Denser stand means faster canopy closure in young plantations and consequently diminishing light conditions for the understorey layer. A significant relation between stand basal area and ground vegetation existed in silver birch plantations but not in two times sparser hybrid aspen plantations (Fig. 4B and C, Table 3). Light conditions in the ground vegetation layer depend on stand basal area and the canopy light transmittance, which in turn may differ among tree species (Messier *et al.* 1998, Comeau *et al.* 2006). Birches and aspens are both light-demanding fast-growing deciduous trees and although their crown architecture is somewhat different, it can be assumed that understorey light conditions in plantations with similar density and basal area are rather similar.

Another significant tree-species-related difference in the current study was the higher concentration of total N in the soil humus layer under silver birch plantations (Table 2). The concentrations of extractable P and K also tended to be higher in the humus layer of silver birch plantations, although these differences were not statistically significant. In the ordination diagram (Fig. 4A), the total N vector pointed to the direction where only vegetation plots from silver birch plantations were presented. Two times denser silver birch plantations produce probably more leaf and root litter than the studied hybrid aspen plantations in a young age. This in turn affects nutrient concentrations in the humus layer. According to several studies the soil microbial activity and the annual rate of net nitrogen mineralization have been found to be high in birch stands compared to conifers or abandoned grassland (Smolander *et al.* 2005, Kanerva & Smolander 2007, Uri *et al.* 2008). However the concentration of total N in the humus layer of the studied former field soils could also have been affected by different fertilization practices during the previous agricultural land use. The vegetation plot mean Ellenberg value for N tended to be higher in silver birch plantations, but this difference was not significant at $p < 0.05$. It can be concluded that denser silver birch plantations start to affect nutrient concentrations in the soil humus layer, and consequently the nutritional status of the ground vegetation, sooner than sparser hybrid aspen plantations. Such a difference is likely to become less pronounced over the course of time, as faster growing hybrid aspen catches up with birch in terms of litter quantity.

As part of the study, the ground vegetation in silver birch and hybrid aspen plantations was analysed from the indigenous *vs.* semi-exotic tree species comparison point of view. No alien vascular plant species were found in the ground vegetation of hybrid aspen plantations. According to previous experience, forest plantations can be established in Estonian conditions without considerable risks of creating favourable habitat for new or previously introduced plant species, contrarily to the situation in some other world regions, e.g. New Zealand and Hawai (Brockerhoff *et al.* 2003, Mascaro *et al.* 2008). In Estonia the extensive dispersal of introduced plant species is hindered by the lack of large-scale open communities and the temperate climate, which means rather slow plant growth (Kukk 1999). At the same time, final conclusions should be drawn cautiously, because the studied plantations were young, and the following vegetation development must show if and when typical forest species will start to appear and if the semi-exotic tree species plantation can sustainably provide habitat similar to indigenous tree species. In the long run, however, the most serious environmental hazard will probably be that the exotic tree species itself turns invasive and spreads out from plantations, and/or crosses with endemic representative from the same genus (Suvanto & Pulkkinen 2004). Also possible mass propagation of new or so far less important pests and diseases could occur (Kasanen *et al*. 2002).

The significantly higher density of silver birch plantations did not result in significantly higher mean BA, although it was approximately 1 m^2 (1.6 times) higher in silver birch plantations. The mean DBH of hybrid aspens was 10% higher as that of silver birches, however the difference was statistically not significant (Table 2). At the same time hybrid aspens had shown individually faster growth while the mean DBH exceeded 4 cm at six out of seven study sites in hybrid aspen plantations and only at three out of six study sites in silver birch plantations (Table 1). The higher planting density for silver birch is recommended for several reasons. It promotes natural pruning ensuring better stemwood quality at final harvest. Silver-birch saplings are less expensive than micropropagated hybrid aspens. Finally, it also helps to compensate the possible loss of trees due to browsing and other damages, which could become a more serious problem in sparse hybrid aspen plantations. On the other hand it results in the need for thinning already at the end of the first decade, otherwise natural competition-driven self-thinning can be expected. Silvicultural practices often impose a disturbance for understorey vegetation development. In the light of the findings from the current study, it brings about a controversy: denser fast-growing silver birch plantations provide conditions for quicker ground vegetation development but also mean additional disturbance in the form of thinning, which as a rule is not planned in the first generation hybrid aspen plantations.

Conclusions

The understorey vascular plant cover in young silver birch and hybrid aspen plantations on abandoned agricultural land was similar in terms of species richness, diversity and ecological characteristics. The anthropogenic disturbances from the previous agricultural land use were recognizable in the floristic traits of the ground vegetation 7–9 years after the plantations were established.

Soil variables as well as overstorey species had significantly affected the understorey vegetation in young deciduous plantations. However, the overstorey impact could mainly be explained by differences in stand densities rather than tree species. In denser silver birch plantations some signs indicated the overall faster development of the ground vegetation, for example, the share of shade tolerant species was higher and the share of half-light and light species was smaller. Also the concentration of total N in the soil humus layer was higher in silver birch plantations, indicating larger litter quantities and higher annual N mineralisation rate. At the same time, the higher density of silver birch plantations brings about the need for thinning, consequently disturbing the ground vegetation, which is something that is not planned during the first rotation in hybrid aspen plantations.

The fact that hybrid aspen is a semi-exotic species did not result in any environmentally unfavourable developments in the understorey vegetation characteristics. No alien species were found and both plantation types had provided similar habitat for indigenous vascular plant species during the first decade after establishment.

Monitoring of the following successional development is planned in the studied vegetation plots in order to provide data on how and when the impact from previous land use, overstorey tree species, physicochemical soil properties and plantation management activities will influence the understorey vegetation in fast growing forest plantations.

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Appendix. The list of most frequent vascular plant species (found in > 10% of the plots), their frequency (*F*, %) and mean coverage in plots where present (*C*, %).

Vascular plant species	Both plantation types		Hybrid aspen plantations		Silver birch plantations	
	F	*C*	*F*	*C*	*F*	*C*
Achillea millefolium	50	4.3	46	5.1	54	3.5
Aegopodium podagraria	12	17.0	7	11.5	17	19.8
Agrostis capillaris	42	5.2	21	7.5	67	4.3
A. gigantea	37	7.3	32	10.7	42	4.2
Alchemilla vulgaris (coll.)	17	1.1	4	1.0	33	1.1
Alopecurus pratensis	12	5.7	0	0.0	25	5.7
Artemisia vulgaris	62	2.9	79	3.5	42	1.6
Betula pendula	23	2.8	36	3.0	8	1.5
Campanula patula	15	1.1	18	1.0	13	1.3
Cerastium fontanum	48	1.4	64	1.5	29	1.3
Cirsium arvense	85	6.0	75	3.5	96	8.2
Dactylis glomerata	17	4.2	11	2.0	25	5.3
Elymus repens	85	10.3	79	10.3	92	10.2
Epilobium montanum	25	1.2	18	1.0	33	1.3
E. parviflorum	21	1.0	39	1.0	0	0.0
Equisetum arvense	23	1.8	29	1.1	17	3.0
Fallopia convolvulus	25	1.0	25	1.0	25	1.0
Festuca rubra	17	15.0	4	2.0	33	16.6
Gnaphalium uliginosum	13	1.3	25	1.3	0	0.0
Hypericum perforatum	17	1.4	32	1.4	0	0.0
Leucanthemum vulgare	27	1.4	32	1.1	21	2.0
Luzula campestris	15	2.0	29	2.0	0	0.0
Lysimachia vulgaris	13	4.1	14	5.3	13	2.7
Matricaria perforata	15	1.1	25	1.1	4	1.0
Medicago lupulina	17	1.9	14	2.3	21	1.6
Mentha arvensis	19	1.0	18	1.0	21	1.0
Myosotis arvensis	50	1.3	43	1.0	58	1.6
Phleum pratense	54	4.3	82	5.0	21	1.4
Pinus sylvestris	12	2.0	7	1.0	17	2.5
Poa angustifolia	25	4.2	14	1.5	38	5.4
P. palustris	19	1.6	14	2.0	25	1.3
P. trivialis	25	2.2	14	1.3	38	2.6
Potentilla anserina	13	1.1	0	0.0	29	1.1
Ranunculus acris	12	1.0	0	0.0	25	1.0
Salix caprea	12	2.0	21	2.0	0	0.0
Sonchus arvensis	42	3.0	54	3.9	29	1.1
Taraxacum officinale (coll.)	83	7.3	79	4.9	88	9.8
Tussilago farfara	37	10.8	39	11.5	33	10.0
Urtica dioica	12	1.5	7	1.0	17	1.8
Veronica agrestis	23	1.2	11	1.7	38	1.0
Vicia cracca	44	1.7	32	1.8	58	1.7
V. hirsuta	40	1.6	46	1.7	33	1.4

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III

Tullus, T., Tullus, A., Roosaluste, E., Tullus, H. 2012. Bryophyte vegetation in young deciduous forest plantations. Baltic Forestry, 18(2), 205–213.

Bryophyte Vegetation in Young Deciduous Forest Plantations

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Abstract

We studied species richness, composition and coverage of the bryophyte layer in young deciduous forest plantations on abandoned agricultural lands in relation to overstory tree species (hybrid aspen or silver birch), land use history (crop field or grassland), site preparation method (whole-area ploughing or strip tillage), and soil properties (moisture, pH, concentrations of N, P and K). The aim of these plantations is to produce pulpwood and energy-wood under the principles of short-rotation forestry. The area under forest plantations is increasing in the region; however their impact on biodiversity is still scantily studied. Previous studies on understory vegetation have focused more often on vascular plants and less frequently on bryophytes. For this experiment, a total of 248 vegetation plots (2 m × 2 m) were established within 62 long-term experimental plots (size 0.1 ha). Thirty eight bryophyte species were found in total, with an average of 1.86 ± 0.11 species per vegetation plot and 4.02 ± 0.26 per experimental plot. The mean coverage of the bryophyte layer was 11.54 ± 2.14%. As expected, typical bryophytes were light-demanding perennials. According to substrate preference the majority of species were either epigeic or generalist. Positive correlation was observed between soil pH and coverage of the bryophyte layer. The impact of land use history and site preparation method on species composition was still evident, since the number of short-living bryophytes was higher in former fields and whole-area ploughed sites. Bryophyte species richness was not affected by overstory tree species in young plantations. Obviously during the further management of plantations the emergence of new substrata e.g. stem bark of bigger trees, leaning stems, branch litter and cutting residues should add diversity to the bryophyte vegetation.

Key words: abandoned agricultural lands, bryophytes, floristic diversity, hybrid aspen, plantation forestry, silver birch

Introduction

The establishment of forest plantations is considered to be an alternative land-use for abandoned agricultural areas in Central and Northern Europe (Makeschin 1999, Weih 2004, Tullus et al. 2012). In commercial forest plantations the production of timber and bioenergy is of primary concern, nevertheless the implications for biodiversity (including floristic diversity) can not be neglected (Carnus et al. 2006, Stephens and Wagner 2007, Brockerhoff et al. 2008, Baum et al. 2009, Bremer and Farley 2010). Studies analysing the understory vegetation of forest plantations on former agricultural land have concentrated mainly on vascular plant species diversity (e.g. Heilmann et al. 1995, Weih et al. 2003). Bryophytes have received less attention; usually they have been analysed together with vascular plants (e.g. Gustafsson 1988 for deciduous plantations and Bråkenhielm 1977, Hill and Jones 1978, Newmaster et al. 2006, Buscardo et al. 2008 for coniferous plantations and French et al. 2008 for deciduous as well as coniferous plantations).

This means that more attention should be paid to bryophytes, since in northern forests bryophytes are dominating constituents of the forest floor vegetation (Newmaster et al. 2006). Moreover, earlier studies (e.g. Herben 1987, Ingerpuu et al. 1998, 2001, 2003, Hokkanen 2006) have indicated that bryophytes and vascular plants may respond differently to environmental factors.

As a rule, bryophyte species richness and diversity increase with the availability of substrata where bryophytes can occur, e.g. ground, bark of living trees, decaying wood and stones (Ingerpuu 2002, Pharo and Beattie 2002, Zechmeister et al. 2003). Most of these structures, except the ground, are represented in very small quantities or are absent on abandoned agricultural lands where forest plantations have recently been established and where big stones have been removed from the topsoil during previous land use. The bryophyte layer is also affected by soil moisture conditions (Proctor 2008). Although bryophytes receive nutrients mainly from precipitation (including leachates from tree canopies and plant leaves), the nutritional properties and pH of the substratum can also be important (Bates 2008). In a study conducted in Pyrenean *Pinus sylvestris* forests, Pausas (1994) found that moss species richness was the highest at intermediate moisture levels and was positively related to soil pH. Correspondence between high soil pH and bryophyte species richness has been observed in several studies in boreal areas (Virtanen et al. 2000, Löbel et al. 2006).

Our previous study on vascular plants in young hybrid aspen plantations on former agricultural land in Estonia (Soo et al. 2009a) showed that soil-related variables (soil moisture properties, pH and nutrient stocks of the soil humus layer) significantly affected understory vegetation of vascular plants, and that species composition was related to previous land use and site preparation method. Short-living ruderals were typical species on former fields and in the case of the more intensive site preparation method (whole-area ploughed sites). At the same time, species richness of vascular plants was higher in plantations where the less intensive site preparation method (strip tillage) had been used. Although we provided a short overview of bryophyte species in this study, we did not analyse the bryophyte layer and its associations with environmental characteristics.

The species richness of vascular plants in the understory of young hybrid aspen and silver birch plantations on former agricultural land was similar (Soo et al 2009b). In the case of bryophytes, several studies have demonstrated the connection between bryophyte species richness and canopy species, which is explained mainly by the differences in throughfall and litter quality (Weibull 2001, Weibull and Rydin 2005). In terms of crown architecture, young hybrid aspen and silver birch trees have some differences. Birch has sympodial branching type (Hynynen et al. 2010) and a tendency to produce sylleptic shoots, resulting in a uniformly dense crown. Aspen has monopodial branching and strong apical control (Remphery and Pearn 2003), which means that leader shoots grow much faster and the emergence and growth of lateral shoots is suppressed. As a result, crowns of young aspen trees are sparser and their light transmittance is higher. Some differences have also been observed regarding litter decomposition rate and chemistry between *Betula* and *Populus* spp. (Moore et al. 2006, Parsons et al. 2008).

The aim of the current study was to describe the formation of the bryophyte layer in young deciduous forest plantations, to provide ecological characterization of bryophyte species common to such sites, and to investigate which environmental factors have influenced the bryophyte layer. Soil-related variables (moisture, pH and nutrient concentrations of the humus layer), previous land use, site preparation method and overstory characteristics (tree species and stand basal area) were included as possible factors explaining variation in bryophyte species richness and coverage.

The following hypotheses were formulated:

i) Among typical bryophytes in the understory of young unclosed forest plantations the proportion of light-demanding open community species is high and the proportion of shade-tolerant forest species is low;

ii) The proportion of bryophytes that prefer deadwood and logs as substrata is low in young forest plantations;

iii) The number of short-living bryophyte species is higher in sites with more intensive cultivation history (former fields and in whole-area ploughed areas) than in sites with less intensive cultivation history (former grasslands and in strip tilled sites).

Material and methods

Study area

The study was carried out in 7- to 9-yr-old silver birch (*Betula pendula* Roth) and hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx) plantations that had been established in 1999 and 2000 on abandoned agricultural land in the continental part of Estonia, with an exception of one silver birch plantation situated on Hiiumaa island (Fig. 1). These stands are aimed at the production of pulp- and energy-wood. The predicted rotation period is 20-30 years for hybrid aspen and 30-40 years for silver birch; during the rotation period one to three thinnings are planned. In the studied young plantations no thinnings had yet been carried out. The mean annual temperature near the studied plantations during a decade before the study was 6.1 ± 0.86 ºC; mean annual precipitation was 630 ± 30.5 mm and the mean precipitation during the growing season (April-October) was 409 ± 31.1 mm (Tullus et al. 2010).

Altogether 24 hybrid aspen and 11 silver birch plantations were included in the study (Fig. 1). One plantation refers here to one real estate property. In these plantations a network of 62 long-term experimental plots (each 0.1 ha) for studying and monitoring the growth dynamics of birch and aspen at various site conditions had previously been created (Jõgiste et al. 2003, Tullus et al. 2007). All silver birch plantations

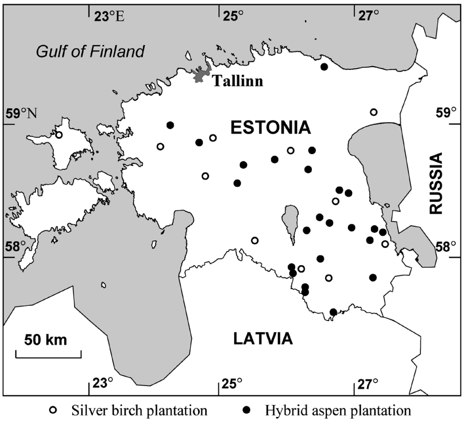

Figure 1. Locations of the studied plantations

were one ha in size and in each of them one experimental plot had been created. The size of hybrid aspen plantations varied from 0.7 to 32 ha. One experimental plot had been established in ten hybrid aspen plantations with uniform site properties. 14 larger hybrid aspen plantations consisted of smaller stands or parts with different soil type and land use history; in those plantations two to five experimental plots had been established. Each plot was located in homogeneous part (based on microrelief and soil type) of the respective plantation or part of the plantation.

Data collection

In total 248 permanent vegetation plots (each 2 × 2 m in size, 4 in each experimental plot) were established for the characterization of vascular plant and bryophyte species cover. Four vegetation plots were distributed systematically across each 0.1 ha experimental plot with two vegetation plots in both sides from the experimental plot centre. The results from vascular plant diversity analyses have been published elsewhere (Soo et al. 2009a, 2009b). As the part of the current study, the list of bryophyte species was compiled and species richness and total percentage cover of the bryophyte layer in each vegetation plot was estimated. Bryophytes were not found on the stems of young trees. Bryophytes not identified in the field were taken to the laboratory for further investigation under a microscope. In a few cases the specimen were juvenile and not fully developed and were identified on a genera level. The nomenclature follows the keybook of Estonian bryophytes (Ingerpuu and Vellak 1998).

The relations between bryophyte diversity and several site characteristics were studied. The plantations were grouped according to tree species, previous agricultural land use and site preparation method used before planting (Table 1). Stand basal area (BA, $m^2\ ha^{-1}$) was estimated in each 0.1 ha experimental plot as the cross-sectional area (over the bark) at breast height in order to characterize the impact of the tree layer (Table 2).

Species richness (S_{vasc}) and coverage (C_{vasc}) of the understory vascular plant layer, estimated in earlier studies (Soo et al. 2009a, 2009b), were used to investigate relations between vascular plant and bryophyte layers.

In order to determine pH_{KCl}, total N, available P and available K in the soil humus horizon (Table 2), soil samples were taken from the centre of each vegetation plot (n = 248). The total N in soil samples was determined by the Kjeldahl procedure. To analyse available P and K in the soil, Mehlich 3 extracant was

Table 1. The distribution of the studied deciduous forest plantations according to overstory tree species, previous agricultural land use and mechanical site preparation method

Planted tree species	Previous land use	Site preparation method	Experimental plots (size 0.1 ha)	Vegetation plots (2 x 2 m)
Hybrid aspen	Crop field	Whole-area ploughing	13	52
		Strip tillage	15	60
	Grassland	Whole-area ploughing	5	20
		Strip tillage	18	72
Silver birch	Crop field	Whole-area ploughing	6	24
	Grassland	Whole-area ploughing	5	20
		Total	62	248

Table 2. Stand characteristics and properties of the soil humus horizon (mean ± standard error, range in brackets) in the studied experimental plots (n = 62) and significance of the differences between two plantation types according to t-test

Variable	All plantations	Hybrid aspen plantations	Silver birch plantations	t-stat	p-value (two-tailed)
Stand density, trees ha^{-1}	1227 ± 62 (640–3070)	1043 ± 27 (640–1540)	2078 ± 164 (1340–3070)	-11.011	**< 0.001**
Stand basal area, $m^2\ ha^{-1}$	1.88 ± 0.23 (0.02–7.29)	1.40 ± 0.17 (0.02–5.33)	4.09 ± 0.73 (0.49–7.29)	-5.385	**< 0.001**
pH_{KCl}	5.7 ± 0.10 (4.0–7.3)	5.8 ± 0.11 (4.1–7.3)	5.6 ± 0.30 (4.0–7.3)	0.524	0.602
Total N, %	0.18 ± 0.02 (0.07–1.36)	0.18 ± 0.03 (0.07–1.36)	0.16 ± 0.02 (0.10–0.29)	0.366	0.716
Extractable P, mg kg^{-1}	84 ± 8.6 (8–403)	81 ± 7.7 (8–291)	100 ± 33.7 (19–403)	-0.843	0.403
Extractable K, mg kg^{-1}	133 ± 9.9 (29–495)	128 ± 10.5 (43–459)	155 ± 27 (29–331)	-1.072	0.288
Moisture[a]	1.6 ± 0.11 (0–3)	1.6 ± 0.11 (0–3)	1.5 ± 0.31 (0–3)	0.603	0.549

[a]soil moisture classes: 0 – excessively well-drained automorphic, 1 – automorphic, 2 – semi-hydromorphic, 3 – hydromorphic

used. The soil pH in 1M KCl suspensions was measured in the ratio 10 g : 25 ml. Analyses were performed by the Laboratory of Agrochemistry of the Agricultural Research Centre in Saku [/http://pmk.agri.ee]. The experimental areas were grouped according to soil moisture conditions, based on earlier studies (Vares et al. 2003, Tullus et al. 2007, 2010).

Data analysis

Light value index was assigned to bryophyte species according to Düll (1991). Based on the system of bryophyte life strategies (During 1992), the studied species were classified into the following categories: species with a life span of a few years (pioneer colonists, colonists, short-lived shuttle) and species with a life span of many years (competitive perennials, perennials, stress tolerant perennials, long-lived shuttle) according to Dierßen (2001). Habitat and substrate preference of bryophyte species was determined based on Ingerpuu et al. (1994) and Ulvinen et al. (2002). Arithmetic mean species richness (S_{bryo}) and coverage (C_{bryo}) of the bryophyte layer were estimated for all experimental plots on the basis of vegetation plot level measures of these variables. In addition, total species richness (ST_{bryo}) of the experimental plot, number of species with a life span of a few years (ST_{short}) and number of species with a life span of many years (ST_{long}) were estimated on the basis of all species found within 4 vegetation plots. Experimental plot-level measures of the analysed traits were used in further statistical processing of the data.

Pearson correlation coefficients were computed between experimental plot-level measures of bryophyte and habitat variables with STATISTICA 7 (StatSoft, Inc. 2004). The effect of tree layer species, land use history, and site preparation method on bryophyte traits was analysed with Student's *t*-test. Both one-tailed and two-tailed results are reported. One-way ANOVA was used to test the significance of differences in means of S_{bryo} , $ST_{bryo,}$ and C_{bryo} between soil moisture groups. Fisher LSD multiple comparison test was applied to determine the significant differences after one-way ANOVA. Normality of the analysed variables was checked with the Shapiro-Wilk's and Kolmogorov-Smirnov test; if necessary, log- or square root-transformation of the variables was used. The mean values are followed by ± standard error in the text. Level of significance $\alpha = 0.05$ was applied in all cases.

Results

Species composition

Altogether 38 bryophyte species (Appendix) and eight taxa identified on the genera level (*Bryum* spp, *Brachythecium* sp, *Riccia* sp, *Dicranella* sp) were found in 221 vegetation plots; in 27 vegetation plots the bryophyte layer was absent. 34 species and eight taxa were found in hybrid aspen plantations and 17 species in silver birch plantations. All observed bryophyte species were common; no rare species were found. The majority of the species were light-demanding species (the most frequent values of light index varied between 6 and 8) (Fig. 2).

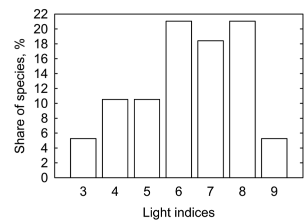

Figure 2. Distribution of bryophyte species according to light index

On the basis of typical habitats, 16 species were species that usually grow in forests, 17 species were species that in addition to forests also grow in grasslands and/or fields, and five species were typical open community species. On the basis of substrate preference the majority of the species were either epigeic or generalists, growing on a variety of different substrata, including usually the ground (Appendix). An epixylic species *Lophocolea heterophylla* can be singled out as an exception.

As hypothesized, ST_{short} was significantly higher in plantations established on former fields and in the case of whole-area ploughed sites (one-tailed *p*-values in Table 3). The species with a life span of a few years (e.g. colonists: *Bryum caespiticum* and *Ceratodon purpureus* and pioneer colonists: *Eurhynchium hians* and *Brachythecium salebrosum*), which appeared more frequently in former fields than in former grasslands were also more frequent in plantations where whole-area ploughing had been applied. ST_{long} did not differ between sites with different land use history and site preparation method.

Species richness and coverage and factors affecting them

S_{bryo} (vegetation plot mean bryophyte species richness) varied from 0 to 6 (arithmetic mean = 1.86 ± 0.11, the most frequent value = 2, Fig. 3a) and ST_{bryo} (total bryophyte species richness within experimental plot) from 0 to 8 per experimental plot (arithmetic mean = 4.02 ± 0.26, the most frequent value = 3). ST_{bryo} was generally two times higher than S_{bryo}, following the linear relationship: $ST_{bryo} = 0.39 + 1.95S_b$ ($r = 0.87$, $p < 0.001$). The experimental plot mean C_{bryo} (coverage of the bryophyte layer) was 11.54 ± 2.14% (range: 0-75%). On 75% of the vegetation plots with an existing bryophyte layer, C_{bryo} was below 10 % (Fig. 3b). On 12 % of the plots, C_{bryo} exceeded 30%.

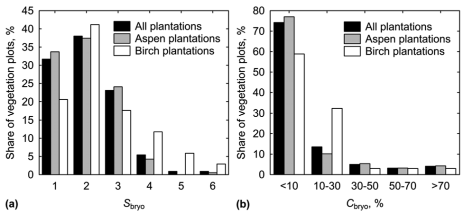

Figure 3. Distribution of vegetation plots with existing bryophyte layer according to a) species richness (S_{bryo}) and b) coverage (C_{bryo}) of the bryophyte layer

Based on two-tailed results of the t-test, there were no significant differences in S_{bryo} , ST_{bryo} and C_{bryo} between plantation groups according to overstory tree species, previous land use or site preparation method (Table 3). C_{bryo} was higher in excessively well-drained soils (Fig. 4). Excessively well-drained soils in the studied plantations were usually stony soils on calcareous parent material (*Leptosols* and *Calcaric Cambisols*) (Vares et al. 2003, Tullus et al. 2007, 2010). S_{bryo} and ST_{bryo} did not differ between soil moisture groups.

Pair-wise correlations between bryophyte and habitat variables indicated the significance of soil pH for C_{bryo}; both measures of bryophyte species richness were positively correlated with C_{bryo} (Table 4).

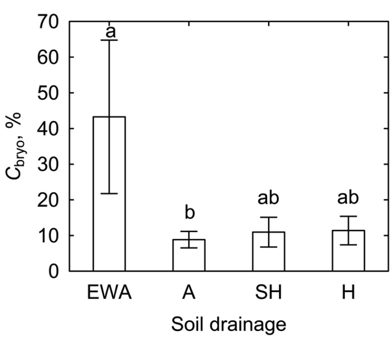

Figure 4. Comparison of C_{bryo} in different soil moisture groups, EWA – excessively well-drained automorphic soils, A – automorphic soils, SH – semi-hydromorphic soils, H – hydromorphic soils. Letters denote significant differences in group means of ln(C_{bryo}) according to Fisher LSD test, whiskers denote standard error

Table 3. Experimental plot mean and total species richness (S_{bryo} and ST_{bryo}), number of long-living (ST_{long}) and short-living (ST_{short}) species and coverage (C_{bryo}) of bryophytes in the studied plantation groups according to overstory tree species, previous land use and site preparation method

Tree layer species:	Hybrid aspen	Silver birch	*t*-stat	*p*-value one-tailed	two-tailed
S_{bryo}	1.84 ± 0.11	1.93 ± 0.41	-0.294	0.385	0.769
ST_{bryo}	3.98 ± 0.26	4.18 ± 0.84	-0.298	0.384	0.767
ST_{long}	2.65 ± 0.23	3.09 ± 0.74	-0.774	0.233	0.466
ST_{short}	1.29 ± 0.18	1.09 ± 0.21	0.518	0.303	0.606
C_{bryo} (%)	11.71 ± 2.43	10.73 ± 4.56	0.174	0.431	0.862
Previous land use:	Crop field	Grassland	*t*-stat	*p*-value one-tailed	two-tailed
S_{bryo}	2.05 ± 0.16	1.62 ± 0.16	1.898	**0.032**	0.063
ST_{bryo}	4.26 ± 0.34	3.71 ± 0.39	1.068	0.145	0.289
ST_{long}	2.71 ± 0.32	2.75 ± 0.35	-0.095	0.463	0.925
ST_{short}	1.53 ± 0.22	0.93 ± 0.18	2.061	**0.022**	**0.044**
C_{bryo} (%)	11.65 ± 2.64	11.40 ± 3.54	0.057	0.478	0.955
Site preparation method:	Whole-area ploughing	Strip tillage	*t*-stat	*p*-value one-tailed	two-tailed
S_{bryo}	1.86 ± 0.19	1.86 ± 0.14	0.026	0.490	0.979
ST_{bryo}	3.97 ± 0.41	4.06 ± 0.32	-0.183	0.428	0.855
ST_{long}	2.41 ± 0.38	3.00 ± 0.28	-1.277	0.103	0.206
ST_{short}	1.55 ± 0.25	1.00 ± 0.16	1.887	**0.032**	0.064
C_{bryo} (%)	11.00 ± 2.76	12.00 ± 3.25	-0.233	0.409	0.817

Table 4. Simple correlations between experimental plot (n = 62) level measures of bryophyte-, vascular plant layer-, overstory- and soil characteristics

	S_{bryo} *r*	*p*	ST_{bryo} *r*	*p*	ln(C_{bryo}) *r*	*p*
S_{bryo}	1.00	-	**0.87**	**<0.001**	**0.65**	**<0.001**
ST_{bryo}	**0.87**	**<0.001**	1.00	-	**0.53**	**<0.001**
S_{vasc}	0.19	0.142	0.21	0.100	0.13	0.299
sqrt(C_{vasc})	0.03	0.817	0.08	0.539	0.08	0.545
ln(Tree density)	0.09	0.547	0.08	0.535	-0.01	0.984
sqrt(Plantation basal area)	-0.07	0.577	-0.12	0.339	-0.07	0.604
Soil pH	0.23	0.075	0.13	0.305	**0.33**	**0.008**
ln(Soil N)	-0.01	0.991	-0.01	0.965	0.12	0.347
ln(Soil P)	0.15	0.238	0.12	0.355	0.09	0.494
ln(Soil K)	0.18	0.168	0.13	0.303	0.23	0.076

Discussion and conclusions

In the studied plantations the formation of the bryophyte layer was still in the preliminary phase, with low percentage coverage and no bryophyte layer on

11% of the vegetation plots. One of the factors inhibiting the formation of the bryophyte layer was probably a thick litter layer (formed mainly by field layer species). Low cover values of the bryophyte layer were also observed in hybrid poplar plantations in NE Germany (Zerbe 2003).

As we hypothesized, the proportion of light-demanding species typical of open communities was high (the most frequent values of light indices 6-8, Fig. 2). In Estonian forests growing in *Aegopodium* and *Oxalis* forest site types, species associated with half-shade habitats dominated (value of light indices 4-5) (Vellak and Paal, 1999). We may predict the likely colonization of new shade-tolerant bryophyte species during the next 10-20 years preceding the planned clearcut. As the majority of the plantations are situated near mature forests, the availability of propagules of forest species should be good.

The average S_{bryo} and C_{bryo} did not differ between plantation groups according to former land use or site preparation method (Table 3). Thus the bryophyte vegetation of the studied young deciduous stands did not show similar response to site preparation as did vascular plant cover of young hybrid aspen plantations, where higher species richness was observed in less disturbed (strip tilled) sites (Soo et al. 2009a). Overstory tree species had no significant effect on the average S_{bryo} and C_{bryo}. However, the distribution of vegetation plots according to C_{bryo} indicated the slightly higher share of plots with C_{bryo} ranging from 10 to 30% in silver birch plantations, although C_{bryo} was below 10% in the majority of plots in both plantation types (Fig. 3b). This could be partly due to the almost two times higher number of trees ha^{-1} and consequently larger stand basal area (BA) in silver birch plantations (Table 2). At the same time there existed no significant relations between stand density or BA and S_{bryo} or C_{bryo} (Table 4). Nevertheless, a higher number of trees could provide more favourable conditions for the bryophyte layer by suppressing competition with the vascular plant layer. In young plantations such developments were in the preliminary phase and were thus difficult to validate with statistical methods.

Soil pH was positively correlated with C_{bryo}, being significantly higher in the soils that have developed on calcareous parent material. S_{bryo} showed a positive trend ($p = 0.08$) with pH. Soils with high pH level are represented in the northern and north-western parts of Estonia, where soils have developed on stony calcareous till on Ordovician and Silurian limestone. These soils are usually dry and had higher C_{bryo} compared to more humid sites (Fig. 4). Soil pH has been found to be a significant variable affecting the distribution of bryophytes on grassland also in other studies in the temperate zone (Virtanen et al. 2000, Löbel et al. 2006). The relation between bryophyte richness and soil pH in the mentioned studies was linear or curvilinear depending on the pH range. In our study, the soil pH range (4.0–7.3, Table 2) did not include extremely acid or alkaline soils. Calcareous soils have been less favourable for the fast growth of trees in the studied plantations due to their high stoniness and small water holding capacity (Tullus et al. 2010). Except the above-mentioned higher C_{bryo} in excessively well-drained soils, there were no other differences in bryophyte traits between soil moisture groups (Fig. 4). A possible explanation is that the moisture regime of wet soils had been improved with drainage during previous agricultural land use and thus the differences in actual moisture conditions between these groups could be smaller than expected from their hydromorphological classification.

The strong cover-richness relation (Table 4) has been observed also in previous studies with bryophytes (Økland 1994, Aude and Ejrnæs 2005). Bryophyte cover of abandoned agricultural lands may thus be used to predict bryophyte richness and site quality for bryophytes.

S_{bryo} was relatively low: on average two species per vegetation plot and four species per experimental plot (based on four vegetation plots). Bryophyte richness is associated with the diversity of available substrata (Ingerpuu 2002, Pharo and Beattie 2002). In our study the majority of the bryophyte species were generalists growing on a variety of substrata, or epigeics growing on soil (Appendix). Substrata such as the bark of large tree trunks, decaying wood and bare rocks were missing in young forest plantations on abandoned agricultural land. In a study conducted in Estonian broad-leaved forests, plot (size 1 m^2) mean S_{bryo} was six, whereas only 42% of all bryophyte species were found on the soil (Ingerpuu et al. 2003). The importance of deadwood and logs as substrata for enhancing bryophyte diversity is emphasized in several studies conducted in boreal forests (Gustafsson and Hallingbäck 1988, Ferris et al. 2000). During the management of plantations, the increasing diameter of tree stems and the emergence of stumps after harvest will offer new habitats for bryophytes. As small-dimensional timber is nowadays valued as energy wood (e.g. Di Fulvio et al. 2011), the share of felling residues left on site after thinnings and final harvests could be rather low. Leaving less-valuable residues on site or keeping some retention trees after harvest would probably be beneficial for bryophyte diversity in plantation forestry systems, providing habitats for epixylic and epiphytic species.

The impact of land use history and site preparation method was still visible in the species composition, as ST_{short} was higher in former fields and in whole area ploughed sites, as we had hypothesized based on the results from the study with vascular plants (Table 3). Further succession should result in a higher impact of the tree layer on the understory, which was insignificant in 7-9-year-old plantations. Further monitoring is needed to clarify whether differences in the bryophyte layer under different overstory tree species will occur. Differences in litter decomposition rate and quality between birch and aspen (Moore et al. 2006, Parsons et al. 2008) could be one factor causing changes in the understory vegetation layer. Probably in the studied young plantations the litter quantities were too small to have a detectable effect on bryophytes. We can expect an increase in richness and abundance of epiphytic bryophytes when plantations are older. According to the study performed in Finnish old-growth forests (Kuusinen 1996), the epiphyte flora on *Betula pendula* was rather poor while the epiphyte flora on *Populus tremula* was unique and characterized by the occurrence of rather specialized species. At the same time it is not known whether hybrid aspen can provide similar habitats for bryophytes as native aspen. The predicted felling age of hybrid aspen is less than 30 years (Tullus et al. 2012), whereas the high diversity of organisms living in association with aspens is observed in old trees.

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МОХОВОЙ ПОКРОВ В МОЛОДЫХ ЛИСТВЕННЫХ ПЛАНТАЦИЯХ

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Резюме

Изучалось видовое разнообразие, видовой состав и проективное покрытие мохового покрова в молодых плантациях лиственных пород из березы повислой (*Betula pendula* Roth) и тополя гибридного (*Populus tremula* L. × *P. tremuloides* Michx) на прежних сельскохозяйственных землях в связи с историей использования земли (бывшее поле или луг), методом подготовки земли (пахотная земля или насаждение в борозды) и с параметрами почвы (влажность, pH, содержание элементов N, P и K). Целью создания таких плантаций является потребность большого количества древесины для бумажной и энергетическтой промышленности за короткий промежуток времени. Площадь таких насаждений увеличивается во всем регионе, но их влияние на биологическое разнообразие до сих пор слабо изучено. Прежние исследования в основном были направлены на изучение видового состава сосудистых растений и в меньшей мере касались мхов. Изучен моховой ярус на 248 пробных площадках (2 м × 2 м), размещенных на 62 постоянных участках (площадью 0,1 га). На пробных площадках найдено 38 видов мхов, средное их число составило 1.86 ± 0.11 на отдельных площадках и 4.02 ± 0.26 на постоянных участках. Среднее проектное покрытие мохового яруса – 11.54 ± 2.14%. Типичными мхами являются многолетние светолюбивые виды. Большинство видов были эпифитные или генералисты, неимеющие предпочтения субстрата. Незначительная позитивная корреляция определена между реакцией почвы и проективным покрытием мохового яруса. Выявлено заметное влияние истории использования земли и ее подготовки на видовой состав мхов так как число кратковозрастых мхов оказалось выше на бывших полях и пахотных землях. Влияние древесного яруса на число мхов было незначительным. По всей вероятности, в течение дальнейшего ухода за плантациями возрастет количество различных субстратов для мхов, из-за чего увеличивается и разнообразие их видов.

Ключевые слова: прежние сельскохозяйственные земли, мхи, флористическое разнообразие, тополь гибридный, лесная плантация, береза повислая.

Appendix. The list of bryophyte species in the analysed vegetation plots, share of plots where the given species was present from all analysed vegetation plots, habitat and substrate preferences and life strategy categories (epigeic – species growing on the ground, generalist – species growing on various substrata, including usually the ground, epixylic – species growing on decaying wood, *c* – colonists, *cp* – pioneer colonists, *s* – short-lived shuttle, *p* – perennials, *pc* – competitive perennials, *ps* – stress tolerant perennials, *l* – long-lived shuttle)

Bryophyte species	Share of plots, %	Habitat	Substrate preference	Life strategy
Eurhynchium hians	39.9	forest, (grassland, field)	generalist	cp
Brachythecium rutabulum	18.1	forest	generalist	pc
B. salebrosum	16.5	forest	generalist	cp
Eurhynchium praelongum	14.1	forest, abandoned field	generalist	p
Plagomnium cuspidatum	10.5	forest	generalist	pc
Brachythecium albicans	10.1	forest, grassland	generalist	p
B. rivulare	7.7	forest	generalist	pc
B. velutinum	7.7	forest	generalist	p
B. mildeanum	7.3	forest, grassland	epigeic	p
B. oedipodium	6.0	forest	generalist	pc
Calliergonella cuspidata	6.0	forest, grassland	epigeic	pc
Rhytidiadelphus squarrosus	4.4	grassland	epigeic	pc
Brachythecium erythrorrhizon	3.6	forest	generalist	p
Cirriphyllum piliferum	3.6	forest, grassland	generalist	pc
Ceratodon purpureus	3.2	grassland, field	generalist	c
Amblystegium riparium	2.8	forest, grassland, banks of water bodies	generalist	p
Atrichum undulatum	2.4	forest, grassland, field	epigeic	s
Plagiomnium ellipticum	2.4	forest, grassland	epigeic	pc
Bryum caespiticum	2.0	grassland	generalist	c
Lophocolea heterophylla	1.6	forest	epixylic	cp
Amblystegium serpens	1.2	forest	generalist	p
Campylium chrysophyllum	1.2	forest, grassland	generalist	p
Barbula convoluta	0.8	forest, grassland, abandoned field	epigeic	c
Brachythecium reflexum	0.8	forest	generalist	ps
Plagiomnium medium	0.8	forest	epigeic	pc
Thuidium delicatulum	0.8	forest, grassland	generalist	p
Atrichum tenellum	0.4	forest, fallow	epigeic	s
B. starkei	0.4	forest	generalist	ps
Calliergon cordifolium	0.4	forest, banks of water bodies	epigeic	pc
Campylium stellatum	0.4	grassland, swamp, mire	epigeic	pc
Climacium dendroides	0.4	forest	epigeic	pc
Eurhynchium pulchellum	0.4	forest	generalist	ps
Hylocomium splendens	0.4	forest, (alvar grassland)	epigeic	pc
Plagiothecium laetum	0.4	forest	generalist	ps
Pleurozium schreberi	0.4	forest, (alvar grassland)	epigeic	pc
Polytrichum juniperinum	0.4	forest, grassland	generalist	ps, pc
Preissia quadrata	0.4	grassland	epigeic	l
Rhytidiadelphus triquetrus	0.4	forest	epigeic	pc

IV

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Understorey vegetation in young naturally regenerated and planted birch (*Betula* spp.) stands on abandoned agricultural land

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Abstract The abandonment of agricultural lands in Northern and Eastern Europe increases the area covered by first generation forests, which are either formed as an outcome of secondary succession or established as plantations. However, questions remain as to how these new stands develop and what kind of species they favour, which in turn has impacts on their ecological and economical value. Our aim was to compare understorey vascular plant and bryophyte vegetation characteristics between naturally regenerated and planted birch stands on abandoned agricultural sites in Estonia, focusing on the aspects of species richness and forest understorey recovery. Species richness and diversity of vascular plants were similar in both stand types but the number of forest vascular plant species was significantly higher in naturally regenerated stands. The bryophyte layer of naturally regenerated stands had a higher species richness, diversity, and number of forest bryophyte species. The higher number of forest vascular plant and bryophyte species in naturally regenerated stands can be explained by the longer undisturbed succession period. The recovery of the forest understorey was unaffected by former agricultural land use (crop field or grassland). The influence of soil properties on the recovery of the forest understorey was not detected, but the number of vascular plant species that grow in forests as well as in grasslands was negatively correlated with distance from forest. Overall, understorey vegetation of natural and planted birch stands did not reveal substantial differences. However, in the case of vigorous natural birch regeneration in the vicinity of forest land, unassisted reforestation should be favoured.

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Introduction

Transitions in land use that result in deforestation for agriculture, or in reforestation of abandoned agricultural lands have taken place throughout the history of human society (Mather and Needle 1998; Lambin and Meyfroidt 2011). Since the nineteenth century, forest transition (a shift from net deforestation to net reforestation) has occurred at different times via assisted or unassisted reforestation in most European countries, as well as in several other countries of the World (Meyfroidt and Lambin 2011). Generally the effect of land use change in the future biodiversity scenarios of terrestrial ecosystems is considered to be crucial (Sala et al. 2000).

One of the most recent examples of forest transition was initiated during the last decades of the twentieth century in Northern and Eastern Europe, when a considerable area of agricultural land was abandoned for socio-economic reasons (Peterson and Aunap 1998; Kuemmerle et al. 2011; Alcantara et al. 2012). In such areas of hemiboreal Estonia, the secondary succession of vegetation that takes place after abandonment leads to the creation of forests with pioneer tree species such as *Betula* spp. among the first arrivers. However, the inclusion of woody species could be slow when herbaceous plants exhibit intensive growth. Birches (*Betula pendula* Roth and *B. Pubescens* Ehrh.) are the most widespread and economically significant deciduous trees in this region (Hynynen et al. 2010). These species have also been used for the establishment of forest plantations on abandoned agricultural lands (Johansson 1999; Liepins 2007). There has been a recent increase in the demand for woody biomass as a renewable energy and pulpwood resource, as well as in the establishment of plantations of fast-growing deciduous trees in Northern and Eastern Europe.

Only a few studies have compared the understorey vegetation characteristics between naturally regenerated and planted stands on abandoned agricultural sites (Aubin et al. 2008; Zhang et al. 2010; Boothroyd-Roberts et al. 2013). The establishment of a monospecific even-aged tree layer, together with silvicultural treatments used for plantation management (e.g. site preparation) creates homogeneous habitat for the understorey. In natural succession, the establishment of woody species has shown a mosaic pattern, creating more heterogeneous conditions for the understorey (Ruskule et al. 2012). Therefore, differences might be expected in the understorey vegetation characteristics of plantations and naturally regenerated stands. In former mining areas in Europe the processes of active reforestation (establishment of plantations) and unassisted natural succession have repeatedly been compared in terms of biomass production and understorey vegetation characteristics (e.g. Prach and Pyšek 2001; Luud and Pensa 2004; Pensa et al. 2004; Tropek et al. 2010), leading to the conclusion that spontaneous succession has its advantages. Besides low establishment costs, spontaneously revegetated sites have exhibited higher natural value (Prach and Pyšek 2001), supporting more diverse vegetation (Pensa et al. 2004), higher species richness and diversity (Hodačova and Prach 2003), and a higher proportion of rare and endangered species (Tropek et al. 2010; Prach et al. 2011). Nevertheless, there are opposite examples; the planting of pine species increased the understorey plant diversity in comparison with unplanted control areas in a degraded Mediterranean kermes oak shrubland (Ganatsas et al. 2012). Regarding tree layer, stand growth and yield characteristics are often better in plantations established with previously selected planting material than in naturally regenerated stands.

In addition to species richness and diversity, species composition is another important aspect that helps to evaluate the vegetation cover. The formation of the tree layer should be accompanied by the gradual recovery of a unique forest understorey. The understorey of recent forest growing on former agricultural land differs from the understorey of forest that was never cleared (Flinn and Vellend 2005; Flinn and Marks 2007), since in young forest the proportion of forest species is low. As migration rates of forest species are usually quite low, distance to propagule sources is an important factor affecting the recovery of the understorey (Dzwonko and Loster 1992; Brunet and von Oheimb 1998; Brunet et al. 2000; Dzwonko 2001; Graae et al. 2003).

Several studies have demonstrated that understorey vegetation characteristics, especially species composition in the forest growing on former agricultural sites, is also influenced by the type of former agricultural use (field or grassland) (Koerner et al. 1997; Wulf 2004; Brunet 2007; Kopecký and Vojta 2009; Soo et al. 2009). The recovery of the forest understorey may be quicker in former grasslands, as a number of forest species often survive with small populations in pastures and meadows, while the colonization of forest species to former crop fields starts only after the cessation of cultivation (Wulf 2004).

Soil chemical properties may also affect the understorey of young forests (Honnay et al. 1999; De Keersmaeker et al. 2004; Graae et al. 2003). Studies from Belgium (Honnay et al. 1999; De Keersmaeker et al. 2004) indicated that soil phosphate content may have an indirect negative effect on the number of forest species, as it stimulates vigorous vegetation development leading to the exclusion of forest species by competitive species. On the other hand Graae et al. (2003) found in a study conducted in Danish oak and beech forests that, instead of soil conditions, limited seed dispersal of forest species was the critical factor explaining the slow migration of some ancient forest species.

The aim of this study was to compare understorey vascular plant and bryophyte vegetation characteristics in planted and naturally regenerated birch stands on abandoned agricultural sites in Estonia and to determine if the recovery of the forest understorey occurs similarly in both stand types. Distance to the nearest forest, the type of former land use, the concentrations of major mineral nutrients and the acidity of the soil humus horizon, the litter layer and overstorey stand characteristics were included as possible factors explaining the variation in understorey vegetation characteristics and the occurrence of forest species.

The following hypothesis was formulated: understorey vegetation of naturally regenerated birch stands is more diverse and supports higher species richness compared to planted stands.

Materials and methods

Study area

The study was conducted in Estonia, which belongs to the hemiboreal forest zone and northern temperate climate zone. Floristic data were collected from 11 silver birch (*Betula pendula* Roth.) plantations and in 11 naturally regenerated birch (*B. pendula* Roth. and *B. pubescens* Ehrh.) stands where 22 experimental plots (each 0.1 ha in size) had been previously created in order to study stand growth and biomass productivity (Vares 2005), (Fig. 1; Table 1). All stands are growing on former agricultural lands that had been

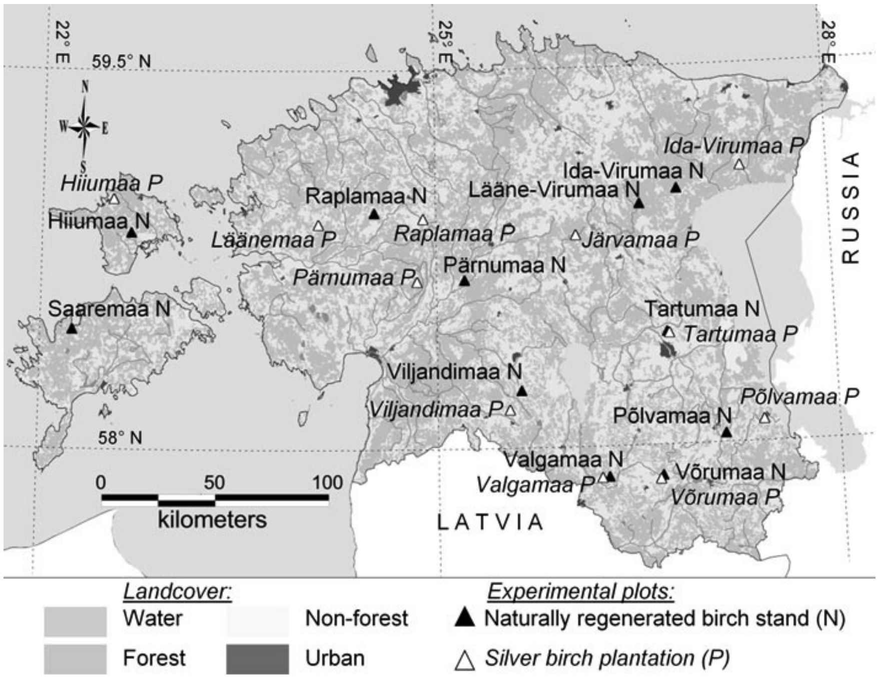

Fig. 1 Locations of the studied birch stands

abandoned in the 1990s. All silver birch plantations were established in 1999 with 1-year-old seedlings. Floristic data analysed in the current study were collected during July of the 13th growing season in 2011. The approximate age of naturally regenerated birch stands at the time of floristic data collection varied between 14 and 20 years, based on an earlier survey of these stands (Vares 2005), although younger birch trees were also present. In every experimental plot, the stem diameter at breast height (DBH) of all the trees was measured and basal area (BA) per hectare was estimated (Table 1). In natural birch stands other tree species were also represented and usually formed the second layer under birches (Table 1). Growing stock and biomass production of planted and natural birch stands was estimated and the respective results are presented in Lutter et al. (2012). In natural birch stands, usually one precommercial and one commercial thinning had been carried out, whereas no management activities had been undertaken in silver birch plantations, except Läänemaa plantation, where light thinning had been done. Using aerial photos (Estonian Land Board 2012), distance from experimental area to the nearest forest was estimated. The type of former agricultural land use (field or grassland) was determined on the basis of personal communication with landowners.

Four vegetation plots (each 2 × 2 m) were created in every experimental plot. In every vegetation plot a list of vascular plant and bryophyte species was compiled, including tree saplings growing in the field layer (defined as the herb and small shrub layer). The total percentage cover of the field layer and bryophyte layer and the percentage cover of individual species were visually estimated, using the scale of 1–100 %. Additionally a list of bryophyte species growing on the trunks of 4 trees situated near the corners of every vegetation plot was compiled. Bryophytes that could not be identified in field conditions were collected for

Table 1 Characteristics of the studied birch stands (distance: distance from the nearest forest, DBH: stem diameter at breast height, BA: basal area; M: volume)

Stand	General		Main tree layer					Secondary tree layer						Total	
	Previous land use	Distance, m	Density, trees ha^{-1}	Height, m	DBH, cm	BA, m^2 m^{-2}	M, m^3 ha^{-1}	Tree spp.	Density, trees ha^{-1}	Height, m	DBH, cm	BA, m^2 m^{-2}	M, m^3 ha^{-1}	BA total	M total
Silver birch plantations															
Hiiumaa	Field	100	1,520	4.7	3.7	2.0	7.7	–						2.0	7.7
Ida-Virumaa	Grassland	40	2,430	11.8	8.5	15.8	95.0	–						15.8	95.0
Järvamaa	Grassland	80	1,760	11.4	9.2	12.8	74.8	–						12.8	74.8
Läänemaa	Grassland	35	1,362	13.5	12.1	16.3	108.3	–						16.3	108.3
Põlvamaa	Field	20	1,960	12.8	9.2	13.4	85.8	–						13.4	85.8
Pärnumaa	Field	400	2,800	11.3	7.8	15.6	90.6	–						15.6	90.6
Raplamaa	Field	250	2,700	12.2	8.6	17.4	107.1	–						17.4	107.1
Tartumaa	Field	60	1,130	10.9	9.4	8.4	47.9	–						8.4	47.9
Valgamaa	Field	40	1,760	10.2	7.1	7.7	41.7	–						7.7	41.7
Viljandimaa	Grassland	150	1,550	12.9	10.5	13.8	88.8	–						13.8	88.8
Võrumaa	Grassland	40	1,740	10.2	8.5	11.0	59.5	–						11.0	59.5
Naturally regenerated birch stands															
Hiiumaa	Grassland	200	5,725	10.5	6.2	20.1	111.0	–						20.1	111.0
Ida-Virumaa	Grassland	100	1,820	9.4	7.3	8.9	45.8	*P. a.*[a]	400	5.3	5.0	0.8	0.6	9.7	46.4
Läänemaa	Grassland	30	3,475	12.0	7.5	16.6	100.5	*P. a.*	7,200	2.3	2.0	2.3	3.9	18.9	104.4
Põlvamaa	Field	40	4,358	11.5	6.8	17.8	104.4	*P. a.*	9,000	2.5	2.0	2.8	3.9	20.6	108.3
Pärnumaa	Grassland	15	9,067	8.7	4.6	16.6	82.3	*P. a.*	11,600	1.6	0.5	0.2	1.5	16.8	83.8
Raplamaa	Field	290	2,638	12.0	9.0	18.8	114.1	*P. a.*	2,500	2.0	1.5	0.4	1.2	19.2	115.3
Saaremaa	Grassland	30	2,844	5.2	2.5	1.6	25.0	*A. i.*[b]	14,000	7.5	6.5	46.5	186.6	48.1	211.6
Tartumaa	Field	155	1,987	11.2	8.8	13.6	78.4	–						13.6	78.4

Table 1 continued

Stand	General		Main tree layer					Secondary tree layer						Total	
	Previous land use	Distance, m	Density, trees ha^{-1}	Height, m	DBH, cm	BA, m^2 m^{-2}	M, m^3 ha^{-1}	Tree spp.	Density, trees ha^{-1}	Height, m	DBH, cm	BA, m^2 m^{-2}	M, m^3 ha^{-1}	BA total	M total
Valgamaa	Grassland	110	2,570	14.2	10.1	22.5	156.7	*P. a.*	2,500	1.7	0.5	0.05	0.3	22.5	157.0
Viljandimaa	Grassland	40	2,773	11.8	7.3	12.9	77.2	*P. a.*	800	0.7				12.9	77.2
Võrumaa	Grassland	90	2,204	13.6	9.4	17.1	114.4	*P. a.*	22,000	2.0	1.5	3.9	10.6	21.0	125.0

[a] *Picea abies*; [b] *Alnus incana*

further investigation under a microscope. The nomenclature follows the keybooks of Estonian vascular plants (Leht 1999) and bryophytes (Ingerpuu and Vellak 1998).

Leaf and branch litter was collected by hand from two subplots (each 20 × 20 cm) located at opposite sides of a vegetation plot. From the same subplots, soil samples were taken from the middle of the humus horizon. Composite samples of litter and soil from each vegetation plot were taken for laboratory analyses. Litter samples were dried at +70 °C to constant weight and weighed to the nearest 0.001 g. Litter estimates (t ha^{-1}) were then calculated for each vegetation plot. The total N in soil samples was determined by the Kjeldahl procedure using method ISO 11261 (1995). To analyse available P and K in the soil, Mehlich 3 extractant was used. Soil pH was measured in 1 M KCl at a 10 g: 25 ml ratio using method ISO 10390 (2005).

Hemispherical (fisheye) photos were taken from the centre of each vegetation plot above the understorey vegetation layer (approximately 50 cm height) using Sigma 8 mm 1:3.5 EX DG FISHEYE lens attached to a Canon EOS 5D digital camera (Canon USA, Inc., NY, USA). The photos were analysed with Gap Light Analyzer 2.0 (Frazer et al. 1999) to estimate canopy openness and the amount of below-canopy (transmitted) direct, diffuse, and total solar radiation incident on a horizontal receiving surface.

Data analysis

Floristic diversity indices

Estimates of species richness of vascular plants (S_{VP}) and bryophytes growing on the ground (S_{B_ground}) and Simpson's diversity index (D'_{VP}, D'_{B_ground}) were calculated for all vegetation plots. In the case of bryophytes growing on the trunks of trees, only species richness (S_{B_trunk}) was estimated. Species richness of bryophytes (S_B) was estimated on the basis of combined data of bryophytes growing on the ground and on tree trunks.

In order to analyse the pairwise relations between species richness, coverage and diversity estimates within the whole univariate dataset, where some non-normality was detected, Spearman correlation coefficients were computed.

Floristic composition

Based on the BIOFLOR database (Klotz et al. 2002) and the Estonian keybook of vascular plants (Leht 1999), vascular plant species were classified by habitat preference into the following categories: forest species, grassland species, fallow species, species growing in forests as well as in grasslands and species growing in grasslands as well as in fallows. Habitat preference of bryophyte species (forest species, grassland species and species growing in forests and in grasslands) was determined based on Ingerpuu et al. (1994). Frequency estimates of bryophytes were determined based on Ingerpuu et al. (2011).

Detrended Correspondence Analysis (DCA, Hill 1979) was applied with default options using PC-ORD v.4 (MjM Software, Gleneden Beach, Oregon, USA); species with less than two occurrences were excluded.

In order to assess species association with stand type (plantations or naturally regenerated stand), Indicator Species Analysis (Dufrêne and Legendre 1997) was performed, including species present in at least eight vegetation plots. Since bryophytes and vascular plants may respond differently to environmental factors (Herben 1987; Ingerpuu et al. 1998, 2001, 2003; Hokkanen 2006), vascular plant and bryophyte data were analysed separately. Combined data of ground and trunk bryophytes was used for ordination where the coverage of trunk bryophytes was considered to be 1 %. The scores of the first three DCA axes were used in further analysis.

In order to understand the ecological data underlying the DCA axes scores, Spearman rank correlations (r_s) were computed with continuous site variables. The effect of discrete factors (stand type and previous land use) on vegetation plot level DCA scores was checked using proc MIXED with SAS for Windows 9.1.3 (SAS Institute Inc., Cary, NC, USA), where experimental plot was treated as a random variable.

Modeling the effect of multiple factors on floristic attributes

Our principal aim was to analyse the effect of stand type (natural or planted) on a number of floristic variables. Being aware of many other factors that potentially might influence these attributes, we included several soil- and overstorey-related variables as explanatory confounders to the model. Stand basal area was considered as the main characteristic of the overstorey effect. Multicollinearity of the continuous explanatory variables was checked based on squared Spearman rank correlations (r_s^2). The results indicated that understorey light characteristics were strongly intercorrelated ($r_s^2 \approx 0.9$) and it was decided to use only total transmitted radiation for modelling.

There were no other strongly ($r_s^2 > 0.5$) correlated variables and they were all included as confounding covariates to the model analysing the effect of stand origin (planted or natural) and previous agricultural land use (grassland or crop field) on species richness and coverage estimates of the understorey vegetation layer.

A generalized linear mixed model with SAS proc GLIMMIX was applied to test the significance of the fixed effects of stand type and independent confounders on floristic attributes. As data was hierarchical (containing both vegetation plot and stand experimental plot level estimates), experimental plot was treated as a random effect. Species richness estimates were treated as response variables with Poisson distribution, while for coverage estimates and diversity indices, Gaussian distribution was used. The assumption of normal distribution of model errors was checked.

Results

Stand and site characteristics

The comparison of stand and site characteristics between naturally regenerated and planted birch stands revealed some significant differences (Table 2). The most significant difference was in the amount of branch litter and thinning residues, and this was three times higher in natural stands compared to plantations where no thinnings had been carried out, and grounded branches originated entirely from litter. As an exception, in the Läänemaa plantation a light thinning had been performed, however the owner had left only minor residues on site, resulting in a just slightly above average estimate of branch litter (1.66 t ha^{-1}). The average amount of leaf litter was similar in both stand types. The mean DBH of birches was higher in plantations, but as natural stands were significantly denser, there was no difference in basal area and volume of the birch layer. In the majority of natural stands a second layer of *Picea abies* had formed, resulting in a higher total basal area. As an exception, *Alnus incana* had overgrown birches in the Saaremaa stand. Canopies had almost entirely closed and light conditions of the understorey layer were

Table 2 Stand and site characteristics (±standard error, range in brackets) and the significance of stand type effect on these variables based on one-way ANOVA for stand-level variables and MIXED model (with stand as random variable) for vegetation plot-level variables

Characteristic	Stand type		Stand type effect, p value
	Plantations	Natural stands	
Determined at stand (0.1 ha experimental plot, $n = 22$) level			
Distance from forest (m)	110 ± 35 (20–400)	100 ± 26 (15–290)	0.814
Main (birch) layer[a]			
Tree density (trees ha^{-1})	1,919 ± 176 (1,130–2,800)	3,587 ± 646 (1,820–9,067)	**0.028**
Height (m)	11.7 ± 0.4 (10.2–13.5)	10.9 ± 0.7 (5.2–14.2)	0.361
DBH (cm)	9.1 ± 0.4 (7.1–12.1)	7.2 ± 0.7 (2.5–10.1)	**0.035**
Basal area (m^2 ha^{-1})	13.2 ± 1.0 (7.7–17.4)	15.1 ± 1.8 (1.6 ± 22.5)	0.371
Stand volume (m^3 ha^{-1})	80.0 ± 7.4 (41.7–108.3)	91.8 ± 10.8 (25–156.7)	0.387
Whole stand (main and secondary layer)[a]			
Basal area (m^2 ha^{-1})	13.2 ± 1.0 (7.7–17.4)	20.3 ± 3.0 (9.7–48.1)	**0.046**
Stand volume (m^3 ha^{-1})	80.0 ± 7.4 (41.7–108.3)	110.8 ± 13.4 (46.4–211.6)	0.065
Determined at vegetation plot (2 × 2 m, $n = 88$) level			
Leaf litter (t ha^{-1})	1.24 ± 0.16 (0.05–4.25)	1.91 ± 0.38 (0.04–9.23)	0.412
Branch litter (t ha^{-1})	1.11 ± 0.12 (0–3.00)	3.41 ± 0.32 (0.36–10.38)	**<0.001**
Soil humus horizon properties			
pH_{KCl}	5.5 ± 0.2 (3.9–7.3)	5.0 ± 0.1 (3.9–7.3)	0.212
Total N (%)	0.16 ± 0.01 (0.09–0.27)	0.13 ± 0.01 (0.06–0.29)	0.236
P (mg kg^{-1})	97.0 ± 13.9 (12.5–372.5	70.3 ± 7.5 (7.5–191)	0.418
K (mg kg^{-1})	141.3 ± 10.6 (18.5–289.0)	105.8 ± 11.2 (13.0–289)	0.269
Understorey light conditions			
Canopy openness (%)	13.9 ± 2.3 (3.8–67.7)	10.3 ± 0.7 (2.6–19.6)	0.459
Transmitted solar radiation			
Direct (mol m^{-2} d^{-1})	1.6 ± 0.3 (0.2–7.9)	1.2 ± 0.1 (0.2–2.6)	0.619
Diffuse (mol m^{-2} d^{-1})	2.1 ± 0.3 (0.7–9.2)	1.8 ± 0.1 (0.5–3.6)	0.682
Total (mol m^{-2} d^{-1})	3.7 ± 0.6 (1.0–16.9)	3.1 ± 0.2 (0.8–5.8)	0.650

Bold indicates significant ($p < 0.05$) effects

[a] Excluding Hiiumaa plantation, as a considerably slower growing plantation, from the comparison of stand growth characteristics

similar in both stand types. Concentrations of main mineral nutrients and the pH of the soil humus horizon were also similar in both stand types.

Species richness and diversity

Altogether 145 vascular plant species and 17 specimens identified at the genera level were found in 88 vegetation plots. Ninety-eight vascular plant species were found growing in silver birch plantations and 116 species in naturally regenerated birch stands; the number of species present in both stand types was 69. Fifty-five percent of the species that were found only in naturally regenerated stands were forest or forest and grassland species; the corresponding figure for plantations was 16 %. Rare and protected species (*Carex* *brizoides, Festuca altissima and Platanthera* sp.) grew on four experimental plots all situated in naturally regenerated stands.

Forty-five bryophyte species were found growing on the ground and on the trunks of bordering trees. Among them 35 bryophyte species were growing on the ground and 24 bryophyte species were growing on trunks, 10 species were found only on trunks. Twenty-five bryophyte species were found growing in silver birch plantations and 36 species in naturally regenerated birch stands; the number of species present in both stand types was 16. The majority of bryophyte species were either very frequent or frequent in Estonia; no rare species were found.

The mean number of vascular plant species in one stand (based on four vegetation plots) was similar in plantations and natural stands (Table 3, one-way ANOVA $F_{1,20} = 0.17$, $p = 0.898$). Vegetation plot-level estimates of S_{VP}, D'_{VP} and C_{VP} were also not affected by stand type (Table 4). The mean number of bryophyte species was significantly higher in naturally regenerated birch stands (Table 3, one-way ANOVA $F_{1,20} = 13.42$, $p = 0.002$). S_{B_ground}, D'_{B_ground} and S_B per vegetation plot were also higher in natural stands (Tables 3, 4). S_{B_trunk} and C_{B_ground} did not differ between silver birch plantations and naturally regenerated birch stands. S_{VP} was negatively affected by tree leaf litter, but other site variables did not significantly affect richness and diversity estimates (Table 4). Pairwise correlations among vascular plant and bryophyte layer characteristics revealed a negative relationship between S_B and C_{VP} ($r_s = -0.37$, $p < 0.001$) and a positive correlation between S_B and C_B ($r_s = 0.47$, $p < 0.001$).

DCA ordination

Axis 1 scores of DCA ordination of vegetation plots with vascular plant data were significantly affected by stand type (Table 5), with silver birch plantations converged to the left side of the axes (Fig. 2). Plot and species scores of natural stands were generally more dispersed. Axis 1 scores correlated positively with stand basal area and litter characteristics and negatively with soil nutrients (Table 6). DCA2 and DCA3 scores were weakly related with distance from forest.

Table 3 Richness (S), coverage (C) and diversity (D') estimates of vascular plants (VP) and bryophytes (B) in the studied birch stands

	Plantations			Natural stands		
	Mean ± SE	Min	Max	Mean ± SE	Min	Max
S_{VP}	12.84 ± 0.73	1	22	13.20 ± 0.91	3	28
S_{VP_4plots}	24.00 ± 1.67	14	30	24.36 ± 2.26	12	36
D'_{VP}	0.70 ± 0.03	0.00	0.94	0.69 ± 0.03	0.05	0.94
C_{VP} (%)	44.09 ± 3.27	2	88	39.07 ± 2.99	1	85
S_B	2.80 ± 0.24	0	7	5.36 ± 0.27	2	9
S_{B_4plots}	6.55 ± 0.74	2	10	10.18 ± 0.66	8	14
S_{B_ground}	1.95 ± 0.17	0	5	4.00 ± 0.29	0	8
S_{B_trunk}	1.43 ± 0.23	0	5	2.36 ± 0.22	0	6
D'_{B_ground}	0.39 ± 0.04	0.00	0.75	0.65 ± 0.03	0.00	0.86
C_B (%)	4.70 ± 0.95	0	25	8.86 ± 1.53	0	40

The effect of stand type on these variables is characterised in Table 4 and in the text

Table 4 Significance (*p* values, type 3 effects) of the factors contributing to species richness (S), diversity (D') and coverage (C) estimates of vascular plants (VP) and bryophytes (B) according to the GLIMMIX model

Factor	Vascular plants								Bryophytes							
	S_{VP}	D'_{VP}	S_{VP_forest}	$S_{VP\_forest\ grassland}$	$S_{VP\_grassland}$	$S_{VP\_grassland\ fallow}$	S_{VP_forest}	C_{VP}	S_B	S_{B_ground}	D'_{B_ground}	C_{B_ground}	S_{B_trunk}	S_{B_forest}	$S_{B\_forest\ grassland}$	$S_{B\_grassland}$
Stand type																
(Plantation)	0.498	0.927[a]	**0.014**[a]	0.328[a]	0.288	0.554[a]	**0.014**[a]	0.627	**0.001**[a]	**0.001**[a]	**0.001**[a]	0.241[a]	0.145[a]	**<0.001**[a]	0.126[a]	0.355
(Natural)	–	–	–	–	–	–	–			–	–	–	–	–	–	–
Former land use																
(Field)	0.632[a]	0.779[a]	0.826	0.918	0.651[a]	0.462	0.826	0.603[a]	0.737[a]	0.322	0.128	0.962	0.055[a]	0.437[a]	0.906[a]	0.102
(Grassland)	–	–	–	–	–	–	–			–	–	–	–	–	–	–
Distance	0.828	0.445	0.232	**0.031**[a]	0.576[a]	0.428	0.232	0.887[a]	0.564[a]	0.488[a]	0.360[a]	0.375	0.496	0.638	0.158[a]	0.732[a]
Basal area	0.475	0.970	0.275	0.062	0.877	0.777[a]	0.275	0.282	0.121[a]	0.112[a]	0.205[a]	0.857	0.102[a]	0.233[a]	0.092[a]	0.091
Transmitted total radiation	0.885a	0.544[a]	0.573[a]	0.308[a]	0.918[a]	0.626[a]	0.573[a]	0.099	0.210[a]	0.103[a]	0.145[a]	0.650	0.341[a]	0.174[a]	0.258[a]	0.066
Leaf litter	**0.030**[a]	0.096[a]	0.294[a]	0.312[a]	**0.034**[a]	0.185[a]	0.294[a]	0.085[a]	0.631	0.601[a]	0.932[a]	0.528[a]	0.407	0.517	0.853[a]	0.285
Branch litter	0.909	0.507[a]	0.478	0.992	0.340[a]	0.346[a]	0.478	0.074[a]	0.525	0.479	0.712[a]	0.896	0.598	0.831	0.362	0.905[a]
Soil N	0.414	0.374	0.838[a]	0.573	0.216	0.628[a]	0.838[a]	0.555[a]	0.642	0.308	0.067	0.735[a]	0.286[a]	0.935[a]	0.556	0.858[a]
Soil P	0.996	0.810[a]	0.345	0.879[a]	0.808[a]	0.631[a]	0.345	0.296[a]	0.302	0.641	0.769	0.551[a]	0.243	0.352	0.257	0.336[a]
Soil K	0.315[a]	0.446[a]	0.148[a]	0.721[a]	0.708[a]	0.689	0.148[a]	0.208	0.820	0.575[a]	0.578[a]	0.663	0.852	0.576	0.850[a]	0.659[a]
Soil pH	0.406[a]	0.635[a]	0.526[a]	0.073[a]	0.353[a]	0.510	0.526[a]	0.915[a]	0.112	0.122	0.752	0.347	0.148	0.210	0.102	0.184[a]

Bold indicates significant ($p < 0.05$) effects

[a] Negative effect

Table 5 The effect of stand type and former land use on vegetation plot-level DCA scores, based on the MIXED model with experimental plot (stand) as random effect

	Stand type (plantation–natural)	*p* value	Former land use (field–grassland)	*p* value
Vascular plants				
$DCA1_{VP}$	−113.6	**0.021**	−31.9	0.549
$DCA2_{VP}$	−64.4	0.111	−27.9	0.509
$DCA3_{VP}$	13.8	0.631	−22.24	0.446
Bryophytes				
$DCA1_{B}$	58.9	**0.012**	11.2	0.661
$DCA2_{B}$	21.8	0.103	19.9	0.145
$DCA3_{B}$	40.3	0.107	47.8	0.055

Bold indicates significant ($p < 0.05$) effects

Axis 1 of DCA ordination with bryophyte data also separated naturally regenerated stands and plantations, and this effect was stronger than in the case of vascular plants (Table 5; Fig. 3). The influence of land use history remained insignificant (Table 5). In addition, bryophyte DCA scores were significantly affected by overstorey stand growth (basal area, branch litter), transmitted solar radiation and soil pH and K (Table 6).

Fig. 2 DCA ordination of vegetation plots and vascular plant species (axis 1 Eigenvalue = 0.82, axis 2 Eigenvalue = 0.63); ellipses indicate 75 % range of the plot scores. Abbreviations: Acer pla *Acer platanoides*, Achi mil *Achillea millefolium*, Aego pod *Aegopodium podagraria*, Agro cap *Agrostis capillaris*, Agro gig *A. gigantea*, Alch vul *Alchemilla vulgaris* (coll.), Alnu inc *Alnus incana*, Alop pra *Alopecurus pratensis*, Anem nem *Anemone nemorosa*, Ange syl *Angelica sylvestris*, Anth odo *Anthoxanthum odoratum*, Anth syl *Anthriscus sylvestris*, Arte vul *Artemisia vulgaris*, Betu pen *Betula pendula*, Betu pub *B. pubescens*, Cala aru *Calamagrostis arundinacea*, Cala can *C. canescens*, Cala epi *C. epigeios*, Camp glo *Campanula glomerata*, Camp lat *C. latifolia*, Camp pat *C. patula*, Care hir *Carex hirta*, Care lep *C. leporina*, Care mon *C. montana*, Care pal *C. pallescens*, Care sp *C. sp*, Care vag *C. vaginata*, Cera fon *Cerastium fontanum*, Cirs arv *Cirsium arvense*, Cirs ole *C. oleraceum*, Dact glo *Dactylis glomerata*, Desc ces *Deschampsia caespitosa*, Dryo car *Dryopteris carthusiana*, Elym rep *Elymus repens*, Epil ang *Epilobium angustifolium*, Epil mon *E. montanum*, Equi arv *Equisetum arvense*, Equi pra *E. pratense*, Fall con *Fallopia convolvulus*, Fest pra *Festuca pratensis*, Fest rub *F. rubra*, Fili ulm *Filipendula ulmaria*, Frag ves *Fragaria vesca*, Fran aln *Frangula alnus*, Frax exc *Fraxinus excelsior*, Fuma off *Fumaria officinalis*, Gale sp *Galeopsis sp*, Gale tet *G. tetrahit*, Gali alb *Galium album*, Gali uli *G. uliginosum*, Gera pal *Geranium palustre*, Geum riv *Geum rivale*, Geum urb *G. urbanum*, Hier umb *Hieracium umbellatum*, Holc lan *Holcus lanatus*, Hype mac *Hypericum maculatum*, Hype per *H. perforatum*, Impa n-t *Impatiens noli-tangere*, Impa par *I. parviflora*, Junc eff *Juncus effusus*, Knau arv *Knautia arvensis*, Laps com *Lapsana communis*, Lath pra *Lathyrus pratensis*, Leuc vul *Leucanthemum vulgare*, Luzu pil *Luzula pilosa*, Lych f-c *Lychnis flos-cuculi*, Lysi vul *Lysimachia vulgaris*, Medi lup *Medicago lupulina*, Mela pra *Melampyrum pratense*, Ment arv *Mentha arvensis*, Moeh tri *Moehringia trinervia*, Moli cae *Molinia caerulea*, Myos arv *Myosotis arvensis*, Oxal ace *Oxalis acetosella*, Padu avi *Padus avium*, Phal aru *Phalaris arundinacea*, Phle pra *Phleum pratense*, Pice abi *Picea abies*, Pinu syl *Pinus sylvestris*, Poa ang *Poa angustifolia*, Poa com *P. compressa*, Poa nem *P. nemoralis*, Poa pal *P. palustris*, Poa pra *P. pratensis*, Poa tri *P. trivialis*, Popu tre *Populus tremula*, Pote ere *Potentilla erecta*, Prim ver *Primula veris*, Prun vul *Prunella vulgaris*, Pyro rot *Pyrola rotundifolia*, Quer rob *Quercus robur*, Ranu acr *Ranunculus acris*, Ranu aur *R. auricomus*, Ranu rep *R. repens*, Rubu ida *Rubus idaeus*, Rume ace *Rumex acetosa*, Rume a-a *R. acetosella*, Saurxcin *Salix aurita* x *S. cinerea*, Sali sta *S. starkeana*, Sali phy *S. phylicifolia*, Sali cap *S. caprea*, Sali cin *S. cinerea*, Soli vir *Solidago virgaurea*, Sorb auc *Sorbus aucuparia*, Stel gra *Stellaria graminea*, Stel med *S. media*, Tara off *Taraxacum officinale* (coll.), Trif med *Trifolium medium*, Tuss far *Tussilago farfara*, Urti dio *Urtica dioica*, Vale off *Valeriana officinalis*, Vero agr *Veronica agrestis*, Vero cha *V. chamaedrys*, Vero off *V. officinalis*, Vici cra *Vicia cracca*, Vici hir *V. hirsuta*, Vici sep *V. sepium*, Viol arv *Viola arvensis*, Viol can *V. canina*, Viol pal *V. palustris*

Species composition

Among all vascular plant species growing on the vegetation plots in the plantations, 53 % were typical grassland species, 22 % fallow species, 13 % forest species, 10 % forest and grassland species and 2 % grassland and fallow species. In naturally regenerated stands 48 % of vascular plants were grassland species, 22 % forest species, 18 % forest and grassland species, 10 % fallow species and 2 % grassland and fallow species. Among all bryophyte species found in the plantations, 52 % were forest species, 39 % were forest and grassland species and 9 % were grassland species. The corresponding figures for naturally regenerated stands were 68.6 % forest species, 25.7 % forest and grassland species and 5.7 % grassland species.

The number of forest vascular plant species (S_{VP_forest}) and the number of forest bryophyte species (S_{B_forest}) were significantly higher in naturally regenerated birch stands, but were not affected by the land use history or the chemical properties of the soil humus horizon (Table 4). Stands and plantations that were situated near old forests contained a higher number of vascular plant species that usually grow in the forest as well as in grasslands ($S_{VP\_forest\ grassland}$). The number of vascular plant species growing in grasslands ($S_{VP\_grassland}$) was negatively affected by tree leaf litter.

The differences in species composition between naturally regenerated stands and plantations were revealed also from Indicator Species Analysis that pointed out 11 vascular plant species characteristic to silver birch plantations, and 8 vascular plant species (including 3 tree species) and 5 bryophyte species characteristic to naturally regenerated

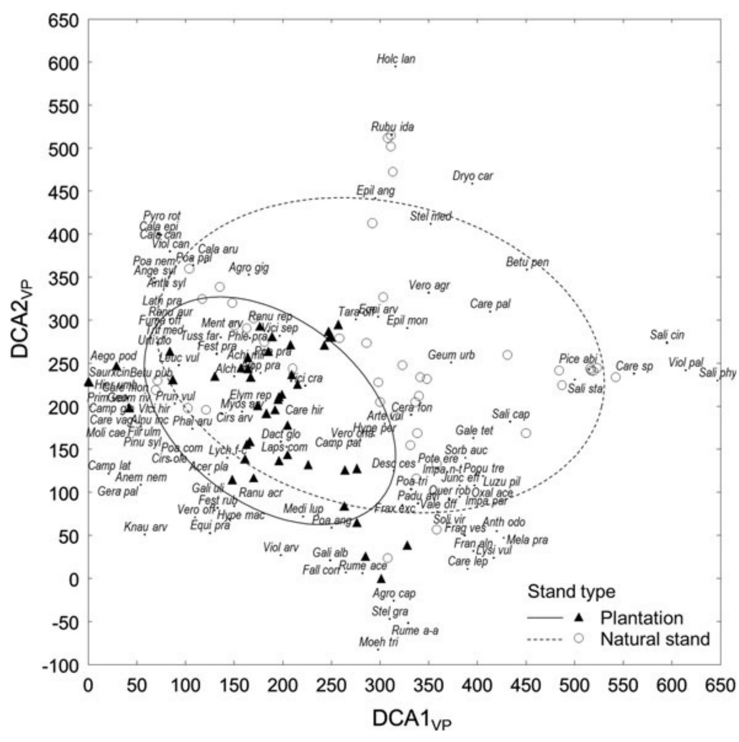

Table 6 Spearman correlation coefficients among DCA axes scores (*VP* vascular plants, *B* bryophytes) and site variables, bold indicates significant ($p < 0.05$) correlations

Variable	$DCA1_{VP}$	$DCA2_{VP}$	$DCA3_{VP}$	$DCA1_{B}$	$DCA2_{B}$	$DCA3_{B}$
Distance	−0.06	**0.27**	**−0.22**	−0.07	0.17	0.16
Basal area	**0.32**	**0.26**	−0.10	**−0.38**	−0.02	−0.03
Leaf litter	**0.28**	−0.13	**0.34**	0.14	−0.18	**−0.22**
Branch litter	**0.43**	**0.31**	0.00	**−0.34**	0.04	−0.07
Transmitted total radiation	0.13	0.02	0.10	0.01	−0.01	**−0.22**
Soil pH	**−0.37**	0.11	**−0.53**	0.03	0.18	**0.27**
Soil N	**−0.37**	−0.07	**−0.27**	0.15	−0.04	0.14
Soil P	0.14	−0.01	**0.26**	−0.01	−0.15	0.07
Soil K	**−0.24**	**0.38**	−0.15	−0.10	0.18	**0.26**

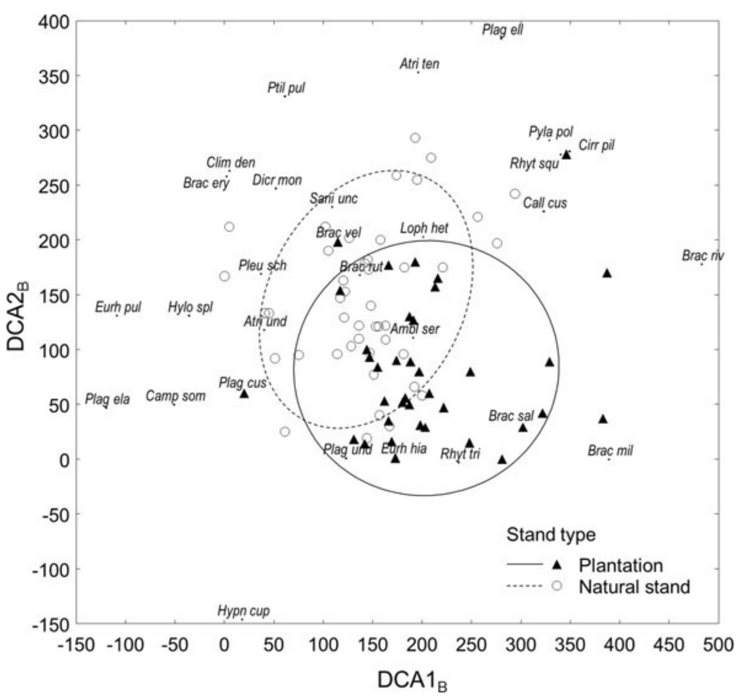

Fig. 3 DCA ordination of vegetation plots and bryophyte species (axis 1 Eigenvalue = 0.59, axis 2 Eigenvalue = 0.40); ellipses indicate 75 % range of the plot scores. Abbreviations: Ambl ser *Amblystegium serpens*, Atri ten *Atrichum tenellum*, Atri und *A. undulatum*, Brac ery *Brachythecium erythrorrhizon*, Brac mil *B. mildeanum*, Brac riv *B. rivulare*, Brac rut *B. rutabulum*, Brac sal *B. salebrosum*, Brac vel *B. velutinum*, Call cus *Calliergonella cuspidata*, Camp som *Campylium sommerfeltii*, Cirr pil *Cirriphyllum piliferum*, Clim den *Climacium dendroides*, Dicr mon *Dicranum montanum*, Eurh hia *Eurhynchium hians*, Eurh pul *E. pulchellum*, Hylo spl *Hylocomium splendens*, Hypn cup *Hypnum cupressiforme*, Loph het *Lophocolea heterophylla*, Plag cus *Plagiomnium cuspidatum*, Plag ela *P. elatum*, Plag ell *P. ellipticum*, Plag und *P. undulatum*, Pleu sch *Pleurozium schreberi*, Ptil pul *Ptilidium pulcherrimum*, Pyla pol *Pylaisia polyantha*, Rhyt squ *Rhytidiadelphus squarrosus*, Rhyt tri *R. triquetrus*, Sani unc *Sanionia uncinata*

Table 7 Characteristic vascular plant and bryophyte species of birch plantations and natural stands according to indicator species analysis, and their habitat preference

Species	Indicator value	*p*-value	Habitat
Plantations			
Vascular plants			
Agrostis capillaris	42.5	0.006	Grassland
A. gigantea	38.7	0.001	Grassland
Alopecurus pratensis	20.5	0.002	Grassland
Cirsium arvense	24.2	0.013	Fallow
Dactylis glomerata	23.2	0.028	Grassland
Elymus repens	59.7	0.002	Grassland
Equisetum pratense	18.2	0.006	Grassland
Festuca rubra	44.6	0.001	Grassland
Galium album	14.4	0.05	Grassland
Ranunculus repens	28.0	0.009	Grassland
Veronica agrestis	19.7	0.048	Fallow
Naturally regenerated stands			
Vascular plants			
Angelica sylvestris	18.2	0.008	Forest, grassland
Fragaria vesca	22.9	0.038	Forest, grassland
Geum urbanum	38.1	0.001	Grassland
Picea abies	58.2	0.001	Forest
Poa nemoralis	18.9	0.012	Forest
Quercus robur	21.2	0.029	Forest
Rubus idaeus	23.0	0.011	Forest
Salix caprea	20.5	0.004	Forest
Bryophytes			
Brachythecium rutabulum	57.1	0.001	Forest
B. velutinum	36.0	0.003	Forest
Lophocolea heterophylla	49.2	0.001	Forest
Plagiomnium cuspidatum	25.4	0.009	Forest
B. erythrorrhizon	22.7	0.001	Forest

Species present at least in eight vegetation plots were included

birch stands (Table 7). The majority of vascular plant species characteristic to naturally regenerated birch stands were forest or forest and grassland species, and all characteristic bryophyte species were forest species. In the case of silver birch plantations, the majority of characteristic vascular plant species were grassland species, with the exception of *Cirsium arvense* and *Veronica agrestis* (fallow species).

Discussion

The current study focused on understorey vegetation of first generation birch forests on abandoned agricultural lands and aimed to clarify the differences that exist in the understorey species richness and species composition between naturally and artificially established stands. We found that species richness and diversity of bryophytes were higher in naturally regenerated stands, thus confirming our hypothesis that naturally regenerated birch forests offer more favourable conditions for ground vegetation. At the same time, species richness and diversity of vascular plants did not differ between the two stand types. Bryophytes and vascular plants have significant differences in morphology and physiology, and differences in the species-richness responses of these plant groups to environmental conditions have also been observed in other studies (Ingerpuu 2002; Ingerpuu et al. 2003).

In contrast to our findings, a study conducted on abandoned agricultural lands in northwest China (Zhang et al. 2010) showed that the herb layer of secondary forests had a higher species richness than that in pine plantations. This can be explained via differences in the tree layer. In our study, tree layer characteristics were quite similar in both stand types (Table 2), while the secondary forests in northwest China had high tree layer diversity (including deciduous trees) in contrast to the monocultural pine plantations. Several studies have concluded that mixed stands may be more beneficial for understorey floristic diversity than monocultures (Barbier et al. 2008; Felton et al. 2010).

Although species richness and diversity of vascular plants were similar in both stand types (Tables 3, 4), DCA ordination with vascular plant data separated plantations and naturally regenerated stands (Table 5), indicating the compositional differences between the two stand types. Species composition of naturally regenerated stands was more heterogeneous (Fig. 2). Tree species (species of *Salix*, *Picea*, *Betula*, *Populus*, *Padus*, *Sorbus*, *Fraxinus, Quercus*) growing in the field layer were typically converged to the region of naturally regenerated stands. Rare vascular plant species were occasionally found only from the vegetation plots of naturally regenerated stands, indicating their more diverse habitat variety. The field layer of naturally regenerated stands had a higher number of forest species than plantations (Table 4) and several forest and forest and grassland species were characteristic to natural stands (Table 7). Thus the recovery of the forest understorey had progressed further in naturally regenerated stands as the colonization of forest understorey species to naturally regenerated stands could start simultaneously with birches after the cessation of agricultural land use. In plantations, however, ploughing was used for site preparation before the planting of birch trees to reduce competition with the field layer. A similar conclusion was reached in the study of Canadian plantations and naturally regenerated stands growing on former agricultural lands (Aubin et al. 2008), where the understorey of plantations was generally less developed than the understorey of naturally regenerated stands. This was attributed to the intensive site preparation method used in plantations.

In the DCA ordination of bryophyte data (Fig. 3) the stand types were separated slightly more significantly than in the case of vascular plants (Table 5). Regarding individual species scores, more species were found in the region of plots from natural stands. Similarly to the vascular plants the number of forest bryophyte species was higher in naturally regenerated stands (Table 4) that could also be attributed to the longer colonization period. Additionally, the amount of branch litter and thinning residues was higher in naturally regenerated stands (Table 2), providing habitat to species that grow on decaying wood. Bryophyte species *L. heterophylla*, *B. velutinum* and *B. erythrorrhizon* that, according to Indicator Species Analysis, were characteristic to naturally regenerated stands are often found on decaying wood (Ingerpuu et al. 1994). The abundance of decaying wood may contribute positively to the species richness of bryophytes, while being less important for the species richness of vascular plants, as demonstrated by Bartels and Chen (2012). In addition, bryophytes and vascular plants interact directly and these interactions may vary from facilitation to inhibition. In our study, a negative impact of the cover of vascular plants on the species richness of bryophytes was observed, which can be related to the competition for available resources between bryophytes and vascular plants and the physical limitation imposed by vascular plant species (Bartels and Chen 2012).

Distance to the nearest forest helped to explain the variation in plot scores of the second and third axes in DCA ordination with vascular plant data. Several studies have concluded that the joint effect of distance to forest and stand age plays a major role in the colonization of vascular plants to recent woodlands (e.g. Brunet and von Oheimb 1998; Jacquemyn et al. 2001; Verheyen et al. 2003). In our study the number of vascular plant species that grow in forests as well as in grasslands was higher in the stands situated near to old forests, but in the case of forest vascular plant species, the correlation was not statistically significant. Possible explanation may be differences in prevailing dispersal types in the case of forest vascular plant species versus forest and grassland vascular plant species in our study. In a study conducted in recent pine woods in southern Poland, Dzwonko (2001) found that, with increasing distance from the ancient woodland, the numbers of anemochores and tree species in the field layer increased, while the numbers of myrmecochores and vegetatively reproducing species decreased. Numerous woody and herb anemochores (*Acer platanoides*, *Alnus incana*, *Alnus glutinosa*, *Picea abies*, *Pinus sylvestris*, *Salix caprea*, *Populus tremula*, *Fraxinus excelsior*, *Athyrium filix-femina*, *Dryopteris carthusiana*, *Pyrola rotundifolia*) represented forest species, and several myrmechochores (*Viola canina*, *Viola palustris*, *Carex montana*) and vegetatively reproducing species (*Aegopodium podagraria*) represented forest and grassland species. This is why the influence of shorter distance was evident only in the case of forest and grassland vascular plant species.

We also studied the effect of land use history and soil properties on the occurrence of forest understorey species. In our study the number of forest species was similar in the stands developing on former grasslands and in the stands on former arable fields. Contrarily, Wulf (2004) found that a large number of forest species occurred more frequently in the stands on former grasslands in northeastern Germany. The possible reason might be differences in land cultivation practices. While Wulf analysed the data collected from stands originating from the nineteenth and twentieth centuries, our stands were established only in the 1990s.

No negative correlation between soil nutrients (N, P, K) and the occurrence of forest species was found, indicating that soil properties do no limit the colonization of forest species to new forests on former agricultural sites in Estonia (Table 4). This is in accordance with the results from Graae et al. (2004), who, based on a seed sowing experiment, concluded that soil variables did not influence the colonization of forest species to recent forests in Denmark. However, the effect of chemical soil properties on vascular plant and bryophyte vegetation was revealed from DCA ordination (Table 6).

We also analysed the effect of light conditions on the understorey vegetation attributes. Somewhat surprisingly, these effects were usually insignificant, except that total transmitted radiation explained some of the variation in DCA axes 2 scores of bryophytes (Table 6). Higher sensitivity to light conditions of bryophytes compared to herbaceous plants was observed also by Tinya et al. (2009). In addition, the understorey is likely to respond to changes in light availability with some delay (Thomas et al. 1999; Brockerhoff et al. 2003), and may therefore reflect historic rather than current light conditions. The studied stand types differed in this respect. In plantations the initial density was about 2,500 trees ha^{-1} which means that the light availability for the understorey was not greatly affected by the planted trees during several years after establishment. In naturally regenerated stands the average density was about 35,500 trees ha^{-1} before thinnings (Jõgiste et al. 2003) and probably the supression of open community species started earlier and the competition for light and nutrients between trees and herbs was stronger.

Regarding tree growth, basal area of both planted and natural birch stands was similar, however, diameter of the stems at breast height was greater in plantations (Table 2). The range of mean heights had been comparable in the same stands also 10 years earlier (Jõgiste et al. 2003). In natural birch stands usually second tree layer of *P. abies* had formed under the dominant birch layer, however its total contribution to aboveground stand volume was less than 9 % (Table 1). A second stand layer can be expected to emerge also in plantations. The establishment of shade-tolerant spruces under pioneer deciduous trees follows as part of the typical natural succession in the region. Growing mixed with spruces is regarded as beneficial for the stem quality of birches (Hynynen et al. 2010). Natural birch stands were quite dense and require repeated thinnings to produce high-quality assortments from large-dimensional stems; on the other hand, if bioenergy production is the aim, then total biomass is more important than individual stems, and from this perspective dense natural stands could outcompete sparser plantations. At the same time, natural afforestation is not always fast and even, and could also result in less valuable tree species than birch. Poor seed availability and competition with a dense herbaceous plant layer on previously fertilized agricultural lands can delay natural afforestation for a period of up to 20 years (Ruskule et al. 2012). From this perspective, planting can be recommended, since trees are able to suppress competition from shade-intolerant plant species and can thereby accelerate the restoration of forest understorey (Fortier et al. 2011; Boothroyd-Roberts et al. 2013). However, the choice of tree species needs careful consideration, as plantations with introduced tree species may lead to reduced plant diversity (Wang et al. 2011).

Conclusion

The need to clarify the consequences of assisted and unassisted reforestation for ecological restoration is relevant to various regions of the world, where forest transition has taken place as a result of changes in agricultural land use. We compared these two alternatives from the perspective of understorey vegetation. Regarding vascular plants, we did not detect a clear trend towards more diverse understorey vegetation in natural birch stands, nor were the stand growth parameters considerably better in plantations. However, observed differences in the understorey species composition between naturally regenerated stands and plantations indicated that the recovery of the forest understorey had progressed further in naturally regenerated stands already 14–20 years after stand creation. In addition bryophyte species richness and diversity were higher in naturally regenerated stands. When the aim is to establish a commercial birch forest on abandoned agricultural land, both natural succession as well as plantation establishment are possible alternatives and they offer quite similar conditions for understorey vegetation. When the aim is to facilitate the restoration of forest ecosystem on abandoned agricultural land, then for areas close to natural forests, natural succession can be recommended. This should result in a mixed stand where colonization with forest understorey species is quite fast. Otherwise the landowner's decision can be based on other aspects like economic goals and landscape context.

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2012–2013	EIC project: "Guidelines for leaving retention trees during regeneration fellings." Principal investigator.
2011–2014	State Forest Management Centre project: "Ecological-economical analysis of shelterwood cutting method and establishment of the network of demonstration-experimental areas." Principal investigator.
2011–2012	EIC project: "Growth development of young deciduous stands on abandoned agricultural land and factors affecting it." Principal investigator.

2011–2012	Baseline financed project 8-2/T9002MIMI: "Forest design studies." Principal investigator.
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2012–2014	KIK projekt: "Valikraie ja kujundusraie juhend." Põhitäitja.
2012–2013	KIK projekt: „Uuendusraiel säilikpuude jätmise juhend." Põhitäitja.
2011–2014	Riigimetsa Majandamise Keskuse projekt: „Turberaiete ökoloogilis-majanduslik analüüs ja näidis-püsikatsealade võrgustiku rajamine." Põhitäitja.
2011–2012	KIK projekt: „Kiirekasvuliste lehtpuunoorendike kasvukäik endisel põllumajandusmaal ja selle mõjutegurid." Põhitäitja.
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2008–2011	ETF grant nr 7298: „Hübriidhaavikute produktsioon ja looduslik mitmekesisus." Põhitäitja.
2006	Sihtfinantseeritav teema nr 0172100s02: „Eesti metsade säästlik ja looduslähedane majandamine." Täitja.
2005–2007	ETF grant nr 6064: „Noorte hübriidhaavaistanduste kasv ja areng." Põhitäitja.

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4. Tullus, A., Lukason, O., Vares, A., Padari, A., Lutter, R., **Tullus, T**., Karoles, K., Tullus, H. 2012. Economics of hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) and silver birch (*Betula pendula* Roth) plantations on abandoned agricultural lands in Estonia. Baltic Forestry, 18 (2), 288–298.
5. Tullus, A., Kupper, P., Sellin, A., Parts, L., Sõber, J., **Tullus, T**., Lõhmus, K., Sõber, A., Tullus, H. 2012. Climate Change at Northern Latitudes: Rising Atmospheric Humidity Decreases Transpiration, N-uptake and Growth Rate of Hybrid Aspen. PLoS ONE, 7(8), e42648.
6. Tullus, A., Kanal, A., **Soo, T**., Tullus, H. 2010. The impact of available water content in previous agricultural soils on tree growth and nutritional status in young hybrid aspen plantations in Estonia. Plant and Soil, 333, 129–145.
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5. Tullus, H., Tullus, A., **Soo, T**. 2009. Hybrid aspen plantations as a new pulp resource in boreal conditions. In: Proceedings of the 2nd Nordic Wood Biorefinery Conference (NWBC), Finlandia Hall, Helsinki, Finland, 2–4 September 2009, 8–11.
6. Tullus, H., Tullus, A., **Soo, T**. 2008. Hybrid aspen plantations as a new biomass resource in boreal Estonia. In: Proceedings of the 16th European Biomass Conference: From Research to Industry and Markets, Valencia, Spain, 2–6 June 2008. ETA-Florence Renewable Energies, 285–289.
7. Tullus, H., Tullus, A., **Soo, T**., Vares, A. 2008. Hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) complex study programme in hemiboreal Estonia. In: Conference proceedings: 23rd Session of the International Poplar Commission, Beijing, China, 26–30 October 2008, 183.
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3. **Soo, T**. 2007. Kõrgem metsanduslik haridus Eestis ja Lätis enne 1920. aastat. Toivo Meikar (Toim.), Metsanduslikust haridusest Eesti Vabariigi eel. Tartu, Eesti Metsaselts, 17–115.

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RASKESTI LÕIKETÖÖDELDAVATE METALLISULAMITE DEFORMATSIOONI KIRJELDAMINE JA MODELLEERIMINE
Prof. **Jüri Olt**
21. detsember 2012

ANDRES MENIND

PECULIARITIES OF PRETREATMENT AND FUELS REFINING OF BIOMASS
BIOMASSI EELTÖÖTLUSE JA KÜTUSTEKS VÄÄRINDAMISE ISEÄRASUSED
Prof. **Jüri Olt**
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LAHUSTUNUD ORGAANILINE AINE JA SELLE ÖKOLOOGILINE TÄHTSUS SUURTES MADALATES VEEKOGUDES
Prof. **Tiina Nõges**, Juhtivteadur **Helgi Arst** (Tartu Ülikool)
28. jaanuar 2013

AIVE LIIBUSK

PRECISE HYDRODYNAMIC LEVELLING USING PRESSURE GAUGES WITH APPLICATION TO IMPROVEMENT OF THE ESTONIAN NATIONAL LEVELLING NETWORK
RÕHUANDURITEL PÕHINEV TÄPNE HÜDRODÜNAAMILINE LOODIMINE RAKENDATUNA EESTI RIIKLIKU KÕRGUSVÕRGU REKONSTRUEERIMISEL
Dots. **Harli Jürgenson**, Prof. **Artu Ellmann** (Tallinna Tehnikaülikool)
22. aprill 2013

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BIOMASS PRODUCTION OF DIFFERENT GREEN MANURE CROPS AND THEIR EFFECT ON THE SUCCEEDING CROPS YIELD
ERINEVATE HALJASVÄETISKULTUURIDE BIOPRODUKTSIOON JA MÕJU JÄRGNEVATE KULTUURIDE SAAGILE
Dots. **Enn Lauringson**, Prof. *emer.* **Hugo Roostalu**
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